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THE AMERICAN NATURALIST

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DEVOTED TO THE NATURAL SCIENCES
IN THEIR WIDEST SENSE

CONTENTS

			Page
I.	Flying-fish Flight, and an Unfixed Law of Nature	LT. COL. C. D. DURNFORD	1
II.	Double Hens' Eggs	PROFESSOR G. H. PARKER	13
III.	Biological Relations of Certain Cacti	DR. W. A. CANNON	27
IV.	Contributions to the Physiology and Biology of the Dugong	PROFESSOR H. DEXLER AND L. FREUND	49
V.	Correspondence: Congress of Oceanographers		73

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All naturalists who have anything interesting to say are invited to send in their contributions, but the editors will endeavor to select for publication only that which is of truly scientific value and at the same time written so as to be intelligible, instructive, and interesting to the general scientific reader.

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INDEX

PAGE

ACMÆA *testudinalis* Müller, Anatomy of. Part I 171
Adaptive modifications of occipital condyles in Mammalia 475
Additional notes on Bahama snakes 229
Additional records for New England Crustacea 141
Affinities of certain Cretaceous plant remains commonly referred to the genera Dammara and Brachyphyllum . . . 189
Allen, G. M. Sowerby's whale on the American coast . . . 357
Alpine Flora of Colorado . . . 861
Anatomy of *Acmæa testudinalis* Müller. Part I 171
Anatomy of *Cryptobranchus alleghaniensis* 287
Andrews, E. A. Egg-laying of crayfish 343
Application of de Vries's mutation theory to the Mollusca 327
Arcella, Preliminary study of finer structure of 797
Autodax lugubris, Capture of at Los Angeles, Cal. 741
Ayers, H. Unity of the gnathostome type 75

BACON, R., *et al.* Congress of oceanographers 73
Baker, F. C. Application of de Vries's mutation theory to the Mollusca 327
Barbour, T. Additional notes on Bahama snakes 229

PAGE

Batrachians of Pennsylvania, New Jersey, and Delaware, Notes on reptiles and . . . 159
Berry, E. W. Living and fossil species of Comptonia . . . 485
Biological relations of certain cacti 27
Blood gills of *Simulium pictipes* 875
Brachiopoda, Old age in . . . 95
Bryant, O. Recent extension of the range of the green crab 382
Burgess, W. S. See Weysse, A. W., and ——.

CACTI, Biological relations of certain 27
Cannon, W. A. Biological relations of certain cacti . . . 27
Capture of the salamander, *Autodax lugubris*, at Los Angeles, Cal. 741
Causes of extinction of Mammalia 769, 829
Cedar Point, Ohio, Naididæ of 683
Cockerell, T. D. A. Alpine flora of Colorado 861
Cole, L. J. A new pycnogonid from the Bahamas 217
Colorado, Alpine flora of . . . 861
Comptonia, Living and fossil species of 485
Condyles, occipital, Adaptive modifications of in Mammalia 475
Congress of oceanographers . . 73
Contributions to the physiology and biology of the dugong . 49

PAGE

Copepoda, Marine, of Rhode Island 639
Copepoda of Massachusetts, Fresh-water 241
Correspondence:
Bacon, R., *et al.* Congress of oceanographers 73
Porsild, M. P. The Danish arctic station 535
Crayfish, Egg-laying of . . . 343
Cretaceous plant remains, Affinities of certain 189
Cryptobranchus allegheniensis, Anatomy of 287
Cushman, J. A. Additional records for New England Crustacea 141
—— Fresh-water rhizopods of Nantucket 371
Cushman, J. A., and Henderson, W. P. Preliminary study of the finer structure of Arcella 797

Dammara and Brachyphyllum, Affinities of certain Cretaceous plant remains commonly referred to the genera . . . 189
Danish arctic station 535
Dexler, H., and Freund, L. Contributions to the physiology and biology of the dugong 49
—— External morphology of the dugong 567
Double hens' eggs 13
Dragonflies in brackish water, Observations and experiments on 395
Dugong, External morphology of 567
Dugong, Physiology and biology of 49
Durnford, C. D. Flying-fish flight, and an unfixed law of Nature 1

Egg-laying of crayfish . . . 343
External morphology of the dugong 567

PAGE

Extinction of Mammalia, Causes of 769, 829
Eycleshymer, A. C. The habits of *Necturus maculosus* . . . 123

Finer structure of Arcella, Preliminary study of 797
Fishes, Notes on Pennsylvania 595
Flora of Colorado, Alpine . . 861
Flow of sap in maple 409
Flying-fish flight, and an unfixed law of Nature 1
Fowler, H. W. Note on Muhlenberg's turtle 596
—— Notes on Pennsylvania fishes 595
—— *Pimephales notatus* in the Lower Susquehanna . . . 743
Fragmental fission, Reproduction by, in Metridium . . . 583
Fresh-water Copepoda of Massachusetts 241
Fresh-water rhizopods of Nantucket 371
Freund, L. See Dexler, H., and ——.

Gills, Blood, of *Simulium pictipes* 875
Gnathostome type, Unity of . 75

Habits of *Necturus maculosus* 123
Hammatt, M. L. Reproduction of *Metridium marginatum* by fragmental fission 583
Headlee, T. J. Blood gills of *Simulium pictipes* 875
Henderson, W. P. See Cushman, J. A., and ——.
Hens' eggs, Double 13
Herrick, J. C. Mechanism of the odontophoral apparatus in *Sycotypus canaliculatus* . . 707
Histogenesis of the retina . . 611
Hollick, A., and Jeffrey, E. C. Affinities of certain Cretaceous plant remains commonly referred to the genera Dammara and Brachyphyllum . . . 189

PAGE

JEFFREY, E. C. See Hollick, A., and ——.

KEPNER, W. A. Notes on the genus Leptophrys 335

LEPTOPHRYS, Notes on the genus 335
Lichens of Mount Monadnock, New Hampshire 661
Living and fossil species of Comptonia 485
Lotus, Variation in number of seeds of 757
Lull, R. S. Volant adaptation in vertebrates 537

MAMMALIA, Causes of extinction of 769, 829
Maple, Pressure and flow of sap in 409
Marine Copepoda of Rhode Island, Notes on 639
Mead, C. S. Adaptive modifications of occipital condyles in Mammalia 475
Mechanism of the odontophoral apparatus in *Sycotypus canaliculatus* 707
Metridium marginatum, Reproduction of by fragmental fission 583
Miller, L. H. Capture of the salamander, *Autodax lugubris*, at Los Angeles, Cal. . . . 741
Mollusca, Application of de Vries's mutation theory to the 327
Morphology, External, of the dugong 567
Mount Monadnock, Lichens of . 661
Muhlenberg's turtle, Note on . 596
Mutation theory, Application of, to the Mollusca 327

NAIDIDÆ of Cedar Point, Ohio 683
Nantucket, Fresh-water rhizopods of 371
Necturus maculosus, Habits of 123
New England Crustacea, Additional records for 141

PAGE

New Hampshire, Lichens of Mount Monadnock 661
New pycnogonid from the Bahamas 217
Notes and Literature:
Anthropology 597
Anthropology, Notes . . . 598
Astronomy and Physics . . 803
Biology 739, 804
Botany . . 143, 461, 600, 814
Botany, Notes, 148, 464, 667, 744, 815
Botany, The Journals, 153, 471, 673, 751, 823
Evolution 456
Exploration 458
Geology 528
Geology, Notes . . . 155, 529
Paleontology 525
Paleontology, Notes . . . 527
Teaching 455
Zoölogy, 137, 375, 593, 741, 806
Zoölogy, Ichthyological Notes, 385, 808
Zoölogy, Notes . 141, 382, 743
Note on Muhlenberg's turtle . 596
Notes on the genus Leptophrys 335
Notes on marine Copepoda of Rhode Island 639
Notes on Pennsylvania fishes . 595
Notes on reptiles and batrachians of Pennsylvania, New Jersey, and Delaware 159
Number of seeds of lotus, Variation in 757

OBSERVATIONS and experiments on dragonflies in brackish water 395
Occipital condyles in Mammalia, Adaptive modifications of . 475
Odontophoral apparatus in *Sycotypus canaliculatus*, Mechanism of 707
Ohio, Naididæ of Cedar Point 683
Old age in Brachiopoda — a preliminary study 95
Osborn, H. F. Causes of extinction of Mammalia . . 769, 829

PAGE

Osburn, R. C. Observations and experiments on dragon-flies in brackish water . . . 395

PARKER, G. H. Double hens' eggs 13

Pearl, R. Variation in number of seeds of lotus 757

Pearse, A. S. Fresh-water Copepoda of Massachusetts . . 241

—— Reactions of *Tubularia crocea* (Ag.) 401

Pennsylvania fishes, Notes on . 595

Physiology and biology of the dugong 49

Picea excelsa, Variations in the pollen grain of 253

Pimephales notatus in the Lower Susquehanna 743

Pollen grain of *Picea excelsa*, Variations in 253

Pollock, J. B. Variations in the pollen grain of *Picea excelsa* 253

Preliminary study of finer structure of Arcella 797

Pressure and flow of sap in the maple 409

Publications received 233, 677, 887

Pycnogonid from the Bahamas, A new 217

RANGE of the green crab, Recent extension of 382

Reactions of *Tubularia crocea* (Ag.) 401

Recent extension of the range of the green crab 382

Reese, A. M. Anatomy of *Cryptobranchus allegheniensis* . . 287

Reproduction of *Metridium marginatum* by fragmental fission 583

Reptiles and batrachians of Pennsylvania, New Jersey, and Delaware 159

Retina, Histogenesis of . . . 611

Reviews:

Alder and Hancock's British Tunicates 379

Bilancioni's Dizionario de Botanica 815

Brooks's The Oyster 377

PAGE

Campbell's Structure and Development of Mosses and Ferns 603

Clements on Leaf Structure . 814

Clements's Research Methods in Ecology 804

Czapek's Biochemistry of Plants 605

Farlow's Bibliographical Index of North American Fungi 146

Freeman's Minnesota Plant Diseases 463

Hantzsch's Birds of Iceland . 139

Harris on Anther Dehiscence 461

Holder's Half Hours with the Lower Animals 140

R. H. and M. A. Howe's Common and Conspicuous Lichens of New England . . 605

Jenks's The Bontoc Igorot . 597

Jordan's Guide to the Study of Fishes 525

Kellogg's American Insects . 137

Kingsley's Elements of Comparative Zoölogy 138

Lacouture's Liverworts of France 608

Lankester's Extinct Animals . 526

Loeb's Dynamics of Living Matter 739

Lotsy's Theories of Descent . 456

McMurry's Special Method in Elementary Science . . . 455

Mayer's Sea-shore Life . . 378

Moore's Universal Kinship . 805

Osterhout's Experiments with Plants 146

Plankton of Northern Seas . 593

Pratt's Vertebrate Zoölogy . 806

Punnett's Mendelism . . . 139

Ries's Economic Geology of the United States 528

Sabine's Manual of a Laboratory Course in Physical Measurements 802

Sargent's Manual of the Trees of North America . . . 148

Schillings's With Flash-light and Rifle 380

PAGE

Scott's Voyage of the *Discovery* 458
Smith's Bacteria in Relation to Plant Diseases . . . 143
Stephens's California Mammals 807
Ward's Flowers of English Trees and Shrubs . . . 463
Weismann's The Evolution Theory 375
Wiesner on Light Intensity 815
Wiesner on Plants and Light 600
Willson's Laboratory Astronomy 803
Rhizopods, Fresh-water, of Nantucket 371

SALAMANDER, *Autodax lugubris*, Capture of at Los Angeles, Cal. 741
Sap in maple, Pressure and flow of 409
Seeds of lotus, Variation in number of 757
Shimer, H. W. Old age in Brachiopoda — a preliminary study 95
Simulium pictipes, Blood gills of 875
Snakes, Additional notes on Bahama 229
Sowerby's whale on the American coast 357
Stone, W. Notes on reptiles and batrachians of Pennsylvania, New Jersey, and Delaware 159

PAGE

Structure of Arcella, Preliminary study of 797
Study, Preliminary, of finer structure of Arcella . . . 797
Sycotypus canaliculatus, Mechanism of odontophoral apparatus in 707

TUBULARIA *crocea* (Ag.), Reactions of 401
Turtle, Muhlenberg's, Note on 596

UNITY of the gnathostome type 75

VARIATION in number of seeds of lotus 757
Variations in the pollen grain of *Picea excelsa* 253
Vertebrates, Volant adaptation in 537
Volant adaptation in vertebrates 537

WALTON, L. B. Naididæ of Cedar Point, Ohio 683
Weysse, A. W., and Burgess, W. S. Histogenesis of the retina 611
Whale, Sowerby's, on the American coast 357
Wiegand, K. M. Pressure and flow of sap in maple 409
Willcox, M. A. Anatomy of *Acmæa testudinalis*. Part I 171
Williams, L. W. Notes on marine Copepoda of Rhode Island 639

THE

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FLYING-FISH FLIGHT, AND AN UNFIXED LAW OF NATURE

C. D. DURNFORD

THE controversy amongst naturalists as to whether flying-fish do or do not flap their wings in flight has become so one-sided as almost to represent extinction — as a controversy.

It is desirable, if possible, to revive it a little, by carrying the argument into new ground: first, because the one side which is at present believed in would appear to be the wrong one; and, secondly, because it seems to have escaped the notice of the other that this is capable of proof.

The arguments, if they may be so called, hitherto in use are simple assertion and denial, and may be summed up into:—

"Flying-fish do fly, moving their wings with extreme rapidity. I have carefully and frequently watched them and there can be no doubt whatever about it."

And the converse:—

"Flying-fish do not flap their wings, but use them as aëroplanes, like swallows when in skimming or sailing flight. I have carefully and frequently watched them, and there can be no doubt whatever about it."

Somewhat similar remarks will be heard in any ordinary group of ship's passengers watching the fish. Some will insist that they see the wings flapping, and some will aver that they are quite still.

But among scientists wing-flapping is undoubtedly very much the under dog and the carefully written paper by Captain Barrett-Hamilton (*Ann. Mag. Nat. Hist.*, ser. 7, vol. 11, p. 389, 1903), also a convinced aëroplanist, perhaps expresses current opinion as well as may be; and even Professor Whitman (*Amer. Naturalist*, vol. 14, p. 641, 1880), who insists that he has seen "distinctly the individual flaps of the large pectorals," adds that this flapping "may be continued for the whole or part of the flight, but it is generally discontinued after the first few rods, and the course continued by a pure skimming or sailing movement"— thus showing that he, too, believes in the possibility of the aëroplane flight.

Proof that such flight by any known species of flying-fish is a mechanical impossibility is the new ground which I propose to take up.

In order to make clear what the aëroplane theory is, I quote from the *Encyclopædia Britannica* (art. "Flying-fish") the "chief results of the inquiries" (*Die Bewegungen der Fliegenden Fische durch die Luft*, Leipzig, 1878) of one of its chief exponents, Professor K. Möbius. These results, which seem also to have formed the groundwork of many subsequent articles, are — with certain omissions on my part for brevity's sake — summed up as follows:—

"They are more frequently observed in rough weather, and in a disturbed sea then during calms; they dart out of the water.... and they rise without regard to the direction of the wind or waves. The fins are kept quietly distended without any motion, except an occasional vibration caused by the air, whenever the surface of the wing is parallel with the current of the wind. Their flight is rapid, but gradually decreasing in velocity, greatly exceeding that of a ship going ten miles an hour, and a distance of 500 feet. Generally it is longer when the fishes fly against, than with, or at an angle to, the wind. Any vertical or horizontal deviation from the straight course, when flying with or against the wind, is not caused at the will of the fish, but by currents of air....in a rough sea, when flying against the course of the waves; they then frequently overtop each wave, being carried over it by the pressure of the disturbed air. They....fall on board vessels. This never happens from the lee side, but during a breeze only, and from the weather side. During the night they frequently fly against the

weatherboard, where they are caught by the current of air and carried upwards to the height of 20 feet above the surface of the water, whilst under ordinary circumstances they keep close to it."

The above is fairly representative of the aëroplane theory. There are, however, several variants to it, the most notable being the addition by later writers of the use of the tail, both as a propeller in air, and also as an explanation of the loud buzzing sound always heard when the fish fly near or over a boat, and which is really made — it seems odd to have to write it — by the rapid whirring of the wings.

Of this whirring or flapping motion Professor Whitman writes: "It is so rapid that it is not easily recognized at any great distance until experience has sharpened the eye." Therein lies, I think, the cause of the birth of the aëroplane theory, though I must add that experience need not necessarily sharpen even good natural sight into being able to see the wing-movement. Knack or chance may come in in such matters. Some time ago, for instance, I was astonished, whilst testing the shooting of a shot-and-ball gun at the butts, to find that in certain lights I could plainly see the ball during its whole flight, whilst the attendant, whose daily business it was to test rifles and guns, and whose sight was far superior to mine, tried over and over again but could not pick it up. So have I seen many watch the whirring wings and declare them to be still.

It is commonly accepted that in matters of observation an affirmative evidence is superior to a negative one. In the special case under consideration, the value of the affirmative true flight evidence is very greatly increased by the fact that the aëroplane contradiction thereof must be in proof of a unique act in nature without a known parallel. Flying lizards and flying squirrels are perhaps the nearest, but in both cases the aëroplane is, I believe, greater by far compared with the weight borne, and — of more importance — the course is certainly far less and falling, not horizontal, or rising, as is that of the flying-fish.

Surely, therefore, it is not too much to ask from the aëroplanists either a reference to some mechanical parallel, or else absolutely overwhelming evidence in favor of the marvellous — a fair expression if no parallel be produced. We do not receive the

evidence, for, as before noted, it consists of a series of witnesses very fairly divided as to whether they can or cannot see the wing-movement, although scientific writers on the subject nearly all follow the latter. We do receive reference to certain parallels, and I shall endeavour to examine these with such lights as I can find. The parallels are, first, the "sailing" or skimming flight of birds (swallows being usually mentioned), and, secondly, parachutes.

For purposes of comparison in this examination, we will take a typical flying-fish. I have the wings of one, which flew on board a steamer on which I was traveling, before me as I write. Its weight was just over a pound, and it had a wing-area of 62 square inches, very liberally computed.

Let us consider the bird-flight first. Concerning this we have certain recognized facts to guide us, for which I refer readers to Professor E. J. Marey's work on *Animal Mechanism* (vol. 2, pp. 221–225, 1874).

We are specially concerned in his acceptance therein of the division of birds into two main classes, *viz.*, those largely given to "sailing" or still-wing flight (which class is found to be endowed with a large wing-surface), and those which confine themselves more to the "rowing" or wing-flapping flight (which, as a class, have short and narrow wings).

"If," says Professor Marey (*loc. cit.*, p. 221), "we compare together two rowing, or two sailing. . .," arranging as far as possible "to have no difference between them except that of size, we shall find a tolerably constant ratio between the weights of these birds and the surface of their wings." Tables are added of this ratio in various birds, as found by dividing the square root of their wing-surface in square centimeters by the cube root of their weight in grammes.

I will from these tables give this ratio for three of the sailing birds and for three of the rowing birds, including the two lowest ratios of the latter. I will add on my own account the ratio for the flying-fish, which is quite properly comparable with birds in this respect.

Name	Weight=p in grams	Surface of wings =$2a$ in sq. cm.	Ratio=$\frac{\sqrt{2a}}{\sqrt[3]{p}}$
Falco palustris.....	208.76	1188	5.810
Falco subbuteo(?).....	509.62	1684	5.138
Hirundo urbica (House martin)	18.00	120	4.180
Columba vinacea.....	112.00	292	3.545
Saxicola œnanthe.....	56.05	125	2.922
Perdix cinerea.....	280.00	320	2.734
Exocœtus (Flying-fish)	453.59	400	2.603

Note the place of the flying-fish. It is quite in its proper position as a very low order of wing-flapper, requiring great wing-speed to sustain it in air. Note also the representative of the swallow tribe, weighing considerably under an ounce, in its proper place in the sailing class. The *Hirundo rustica*, or swallow proper, would doubtless hold a higher place still — our principal parallel, whose featherweight ought to have protected us from the comparison.

The figures should be convincing; I will not, therefore, comment more upon this, but proceed to another test, *viz.*, to find what size of wing a one-pound (453 grams) fish would require to raise it into the sailing class. No birds are dealt with by Marey of exactly one pound weight; I will therefore take the next above and the next below that weight.

The *Falco subbuteo* above shown has a weight of 509 grams and a wing-area of 1684 sq. cm., with ratio of 5.138, and the *Corvus cornix* has a weight of 374 grams and a wing-area of 1156 sq. cm., giving a ratio of 4.717.

Our one-pound flying-fish, to enable it to sail, would thus require a wing-area between three and four times greater than the 400 sq. cm., which it possesses. And, mark this, even then it would only sail as birds sail, in favorable winds and circumstances, falling and rising and using the "rowing" flight frequently, as may be necessary, not as our fishes go, "without regard to the direction of the wind," horizontally, and close to the water, and, according to aëroplanists, with ever still wings! Further, "concave bird-like surfaces afford from 3 to 7 times as much support as

planes." (*Encycl. Brit.*, art. "Aëronautes,—re flight.") It has been pointed out to me that it is extremely improbable that a flying fish's wings can assume this concave shape. If this be so, "from 9 to 28" may be substituted for "between three and four" times, above.

Need I go on? I am afraid so — superstitions, especially learned ones, die hard. So to the second parallel offered us, the parachute. The term implies the act of falling through the air, and not the horizontal or the rising motion with which we are dealing. Still, the word has been used in explanation of the fish's supposed deeds, and I will try to deal with it and at the same time keep clear of the pitfalls which will surround the effort.

Professor Möbius puts the speed of the flying-fish as "greatly exceeding that of a ship going 10 miles an hour." George Bennett (*Wanderings in New South Wales*, vol. 1, p. 31, 1834), much quoted, puts its extreme time in air at 30 seconds "by the watch," and its distance at 200 yards; this works out at rather over $13\frac{1}{2}$ miles an hour, extreme rate. It will, perhaps, give a sufficiently large margin to call the fish's average speed 15 miles an hour.

Now if wind and a body, either or both in motion, meet at a rate of 15 miles an hour directly against each other, the body having 1 square foot of surface, the pressure exerted thereon will be 1.107 lbs. That, I think, implies that if a flying-fish weighing a little over a pound and having a wing-surface of 144 square inches (an impossibly large one, of course, for such a fish) were falling through still air, it would descend at the rate of about 15 miles an hour; or, on the other hand, if it were in a wind blowing 15 miles an hour straight upward from the sea (an impossibly favoring wind, of course) it would just be supported. I will leave it entirely to my readers to imagine the effect in the second case upon our fish of reducing its wing-area from the suppositious 144 sq. inches to its actual 62 sq. inches.

If the reader's imagination is not sufficient to drop the fish into the sea at once by the reduction, then let him add the effect of removing as much support as would be taken away by changing the impossible upward-blowing wind into the ordinary horizontal one at the same 15 miles an hour speed, meeting the wings at an acute angle. There are pitfalls here, so I will avoid angles and

calculations, and merely point out that, however much scientists may differ as to the amount of the loss of the supporting power involved, none will dispute that there will be a very great loss.

Yet again, if these descents from favoring suppositions to sober facts will not convince, I must advance one more argument. It is, I believe, like the others, new ground, and I will give it a fresh paragraph.

Flying-fish, at the end of their first flight of usually about 10 to 50 yards, have a habit, especially when approaching the crest of a wave, of momentarily checking their wing-movement and slowing down from the blur of great rapidity into a pace in which the flapping of the wing becomes easily visible. This period of visibility is supposed by aëroplanists to be the only portion of the flight during which the wings move, and they even deny them at this time any supporting power whatever. It is their "period of occasional vibration" or "fluttering," and their explanation thereof will make a mechanician smile or feel sad, according to his temperament. I have already quoted it from Möbius, and it amounts to the wings trailing in the wind like a loosely flapping flag, thus not only depriving the heavy fish of the so called support of its miniature aëroplanes, but actually converting them into an active drag.

And yet, according to the theorists, at an extreme suggested speed of 13½ miles an hour, the fish still sails!

Such an upsetting of one of the best known of nature's laws as all the foregoing implies would be impossible of final acceptance, even if we could not, as many of us can, see the flying-fish flying.

I studied the "vibration" or flutter periods very carefully this spring when returning from the Gulf of Mexico. Their object and method seemed simple and clear, and to be as follows: the slowing down from extreme wing-speed into visibility heralds an immediate increased effort of flight, often, if not usually, to enable the fish to surmount a wave. The fish is, in fact, pulling itself together for a spurt. The flutter, as was to be expected, is accompanied by a slight fall of the fish of perhaps 2 or 3 inches; but the spurt, at once put on, regains the lost elevation and lifts the fish well over the obstacle. This sudden rise of the fish (the "frequently overtop each wave" of Möbius) is constantly to be seen, and to many the wings seem still at this time.

The difference in the rates of speed of wing-flapping on different days is very marked. At times, and often for many successive days, it is noticeable that, although the bodies of the fish as they rise from under the steamer's bows are clearly and sharply defined their supporting wings have a peculiar hazy and blurred look, with a want of definition of outline which cannot be accounted for, for they seem to be still. Then a day will come when the fish, still fleeing in front of the ship, will move their wings less rapidly and their motion will become plainly visible. There are still many lookers-on who cannot pick it up, but for the rest the aëroplane theory is exploded for ever, and when next the swifter-moving wings are seen with the eye of knowledge the wonder is that there had been any difficulty. The haze and blur are exactly what should have been looked for under the circumstances.

We have all of us watched sea-gulls soaring quietly in a certain direction, but obliged to flap when they turn away, the vigor of the flapping varying more or less regularly with the direction in which they meet the wind. It is more than probable that the change of wing-speed of the fish varies for similar reasons in degree of rapidity, soaring being, as I have endeavored to show, quite out of the question. From whatever cause, it certainly does so vary.

A curious thing about the "vibration" periods is that they seem to offer fleeting glimpses of a satisfactory wing; for a moment, now and again, the wings have outlines and edges, and will also occasionally return a sun-glare to the eye from their wet glassy surfaces, such as might be expected from them when not whirring. Such a glare is also now and then momentarily to be seen when a fish ceases flying, and just before it strikes the water, if it be in the proper position with regard to the sun. There would, of course, be many long periods of this glare were the wings really still.

One or two more prominent fallacies are handed on from writer to writer, and often accepted as facts. One is that the fish are helped in their flight by the distention of their air-bladder. If such had any appreciable effect it would be that of impeding the flight, for the contained air being under compression would be denser and therefore heavier than the outside air, and the increased

size of the fish would merely check its speed as a hollow bullet is checked.

Steering-power is also denied to the fish by most naturalists. It is, nevertheless, a matter of common seafaring knowledge that they turn with deliberate intention. I have myself watched one fly towards the ship, and, circling back, finish its flight in a direction straight away from the ship. It approached within a yard or so of the side, close under where I was standing. The check of speed on its first taking alarm was marked, and during the turn of half a circle of about 10 or 12 feet radius which it made it could not have been flying at a rate of more than three or four miles an hour.

Again, they rise quite at will, though this power also is denied by aëroplanists. With reference to this, as well as to their power of steering, the late Earl of Pembroke, or Doctor G. H. Kingsley, joint authors of *South-Sea Bubbles*, says (p. 64, 7th ed., 1895): "Flying-fish *do* fly, moving their pectoral fins with extreme rapidity, moreover, they raise and lower themselves over the tops of the waves, and do *not* dip into them,. . . . I remember between Panama and Rapa I used to see the cabin's bulls' eyes surrounded by a circle of scales every morning left there by flying-fish." They were making for the light. No ingenuity can fasten this upon "currents of air," which are credited with so many other impossible feats on behalf of these fish. This habit of theirs is quite well known, and is effected by raising themselves and steering, pure and simple.

Their taking a baited hook is also denied. As a matter of fact, a baited hook is the first part of the fishing-process of the Barbados flying-fishing fleet, with which I have been out. We had a blank day; but, according to the animated description of the boatmen, the struggles of the first victim bring round it swarms of sympathizers (as gulls flock round a wounded companion), and these are "raked" into the boat by the hand hoop-net, an enlarged edition of a round shallow shrimp-net without any handle.

I have throughout this paper spoken of flying-fish generally, for the wing-areas of all of the known kinds are to their weights and speeds such that the impossibility of their practical use as aëroplanes differs only in degree.

Flying-fish put on different aspects according to the state of air and sea. One is rather startled at times by the changes in their methods. In oily equatorial calms, I have watched them in numbers flying long distances with their tails in the water and their heads and wings in the air, the body making an angle of perhaps 30° or 40° with the horizon. The wake left in the water by the dragging tail showed, as well as I could judge, no signs of its having been used for purposes of propulsion, even in its own element, and it is, perhaps, simply to relieve the fish of its weight that it is so supported when there is no fear of the wings being caught by ruffled water; nevertheless the peculiar long lower half of these tails specially adapts them for use as auxiliary propellers to a fish which, with their exception is "a fish out of water"; and it looks so like a case of natural evolution, that I feel inclined to doubt the justice of my personal observation as to their non-use.

It would seem, from this habit, reasonable to suppose that the fish have the power of flapping their wings at various angles, as have birds, as ordinarily their bodies are fairly horizontal as they fly.

The flight of these fish is often described as "graceful," "light," and so on. To him who believes that they soar along easily for 200 yards without further effort than a preliminary leap from the sea, such an opinion may be a natural one.

To him who recognizes that such a leap is mechanically impossible, whether or not assisted by a continuous tail-movement, or to him, who, without thinking particularly about it, simply sees the heavy laboring of the wings as the fish patiently whirrs along its even, uneventful way, "graceful" and "light" are terms misplaced. Strenuous, persistent, plodding effort is the impression left upon the mind, the least failure in which effort means plumping into the water. One often sees this happen obviously without intention on the fish's part.

In conclusion, it is, I think, made clear:—

1. That flying-fish would require to have a wing-area several, and probably many times greater, according to their weights, than they actually possess to enable them to accomplish sailing flight in even such a restricted form as that carried out by sailing birds.

2. That we know of no parallel case in nature which would justify the assumption that the possession by these fishes of even such increased wing-area would of necessity enable them to sail long distances —(*a*) horizontally, or (*b*) close to an obstruction (the sea), or (*c*) in defiance of the direction of the wind; much less all three (*a*), (*b*), and (*c*) combined, as they commonly fly.

3. That their common flight is exactly what is to be expected of flyers holding, as they do, a very low wing to weight ratio — flyers capable of and of necessity employing, extreme wing-speed.

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CONTRIBUTIONS FROM THE ZOÖLOGICAL LABORATORY OF THE MUSEUM OF COMPARATIVE ZOÖLOGY AT HARVARD COLLEGE. E. L. MARK, DIRECTOR. No. 173

DOUBLE HENS' EGGS

G. H. PARKER

THE presence of an additional yolk or of a second more or less perfect egg in a hen's egg, though not an unusual occurrence, is rare enough to excite the attention of those interested in natural phenomena and has been a matter of record since the time of Aristotle. A recapitulation of the early instances of this kind has already been given by Davaine ('61), who has also added much to our knowledge of double eggs. The following account contains a description of five such eggs which have come to the writer's notice in the past few years and present certain features worthy of record.

Of these eggs the first to be described was laid 26 June, 1905, by a hen belonging to Mrs. Prince Stuart of Wood's Hole, Mass. I am indebted to Mr. A. S. Pearse for the opportunity of examining it. The egg was unusually large, its major axis measuring 74 mm., its minor 55 mm. In form it was not unlike a normal egg except that the point was less certainly distinguishable from the butt than is commonly the case. The shell was almost white; near the poles its surface was smooth, but about its equator there was a broad band of unusual roughness. Within was a normal shell membrane inclosing a single mass of albumen containing two yolks. These lay one toward the butt, the other toward the point of the egg. The one toward the butt was approximately spheroidal with its major axis at right angles to that of the whole egg. It measured 34 mm. by 30 mm. The yolk nearer the point was smaller than the other one, by which it was indented on the side away from the point. It measured 21 mm. by 27 mm., and its major axis was also at right angles to that of the whole egg.

Though the two yolks were in intimate contact along their applied faces, they were organically distinct, since each possessed an independent vitelline membrane. So far as could be judged, they were of the same age, in that both had the appearance of freshly laid yolks.

The second egg to be described is one that I had the privilege of examining through the kindness of Mr. C. C. Spratt. It had been laid in the spring several years ago by a hen belonging to Mrs. C. H. Gould of North Bridgton, Me. The outer shell, which was thick but otherwise normal, was much broken; its two axes measured 54 mm. and approximately 73 mm. It was lined with a shell membrane and its contents were lost except for a small complete egg which it contained. This measured 33 mm. by 39 mm., and, though rather roundish in outline, it presented a butt and a point. Its shell was thinner than usual and its whole outer surface was granular. The inside of this shell was lined with a shell membrane and contained dried albumen and a dried yolk.

The three remaining eggs were laid by a hen belonging to Mr. F. Nielson of Medford, Mass. They were laid in March, 1903, and shortly after the laying of the largest one the hen died. When the eggs came to my hands, each had a small opening at one end. I am therefore unable to give their exact length but in other respects they were in excellent condition for examination. The smallest measured 43 mm. by approximately 57 mm., the next 48 mm. by approximately 56 mm., and the largest and last to be laid 55 mm. by approximately 71 mm. In each instance a point and a butt could be distinguished and the shells were of normal texture, color, and thickness. Each shell contained a shell membrane and a mass of albumen in which was imbedded a second smaller egg.

These eggs were used for exhibition purposes, but I was allowed to cut open the one of intermediate size, and the appearance of its section face is given in the accompanying figure. It will be seen at once that the inclosed egg is relatively large; it measured 45 mm. by 29 mm. A butt and a point could be easily distinguished on it. The chief axis of the small egg was parallel to that of the large one and its point and butt were just within the corresponding

parts of the inclosing shell. The shell of the small egg was rather thin; it was lined with a shell membrane and contained albumen which had withdrawn slightly from the shell wall, probably through shrinkage. Between the inner shell and the membrane lining the outer shell, was a mass of albumen, which was slightly discolored around the equator of the smaller egg and near its butt by a small amount of yolk substance. Aside from this neither the larger nor the smaller egg contained any evidence of yolk.

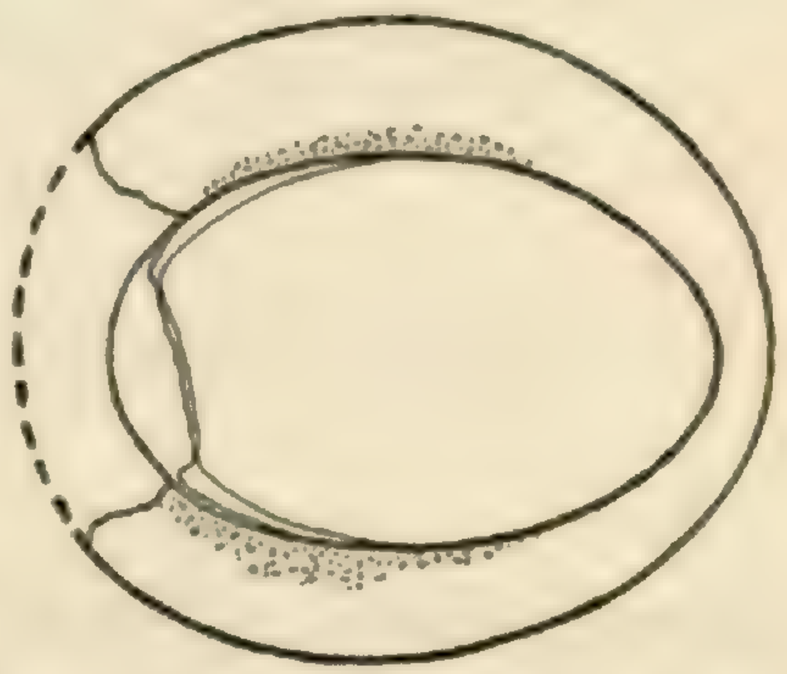

FIG. 1.—A double egg cut in longitudinal section from butt to point. The outer shell measured 48 mm. by about 56 mm.; the inner, 29 mm. by 45 mm.; both contained albumen, that of the inclosing egg showing yolk substance (drawn as granules in the figure). Beginning at the butt of the egg, the dotted line represents the reconstructed shell: the first solid line, the shell of the inclosed egg; the second, its shell membrane; and the third, the surface of its albumen. The spaces between shell and membrane, and membrane and albumen, are probably due to shrinkage.

The internal condition of the other two eggs belonging to this set could not be ascertained, for the owner preferred to keep them in their present form. Judging, however, from what could be seen through the small holes in their ends, they contained relatively large eggs with firm limy shells like that seen in the egg that was cut.

An examination of the five eggs thus far described and a comparison of their conditions with those of other recorded cases of double eggs, have led me to the conclusion that at least two factors are concerned in the production of such eggs. Double-yolk eggs like the first one described, are due in my opinion to the simultaneous or almost simultaneous discharge of *two* yolks from the ovary instead of *one*, these two being enveloped by albumen, shell membrane, and shell in an essentially normal manner. Inclosed eggs on the other hand may be the product of an entirely normal ovary and may result from the abnormal action of the oviduct, in that a yolk normally supplied by the ovary may be abnormally covered, retained, and inclosed in another egg. Thus two factors in the production of double eggs may be distinguished: ovarian and oviducal.

That these two factors are really independent is indicated in several ways. First, they seem to come into play at somewhat

different seasons. The double-yolk egg described in this paper was laid in June, and, though Bauer ('98, p. 304) and Immermann ('99, p. 7) record cases of this kind in December and Panum ('60, p. 186) in January, the great majority of such occur during the warmer part of the year, from May to August according to Immermann ('99, p. 7) or from March to September according to Panum ('60, p. 186). The inclosed eggs on the contrary are produced in the winter and spring. Thus the second egg described in this paper was laid at some time in the spring and the remaining three in March. A compilation of the published records of this kind shows the period to extend from December to March or April.[1] It therefore appears that while double-yolk eggs may be laid at any time of year, they are most abundant in summer and that inclosed eggs, so far as the records go, are limited exclusively to the winter and spring.

Another point in evidence of the independence of the ovarian and oviducal factors is seen in the condition of the hen. The laying of eggs with two yolks may become, as Landois ('78, p. 24) declares, almost habitual with certain hens. Bartels ('95, p. 143) states that the hen that laid the double egg described by him had often laid such eggs and Immermann ('99, p. 8) records the case of a hen that laid such an egg about every eight days. Apparently this is as much an organic peculiarity of certain hens as is the production of twins by certain individuals in the human species, and, while it may be called abnormal in that it is unusual, it is in no sense indicative of serious organic derangement or disease. The laying of inclosed eggs, however, is often followed by serious consequences to the hen. Thus the hen belonging to Mr. Nielson died shortly after laying the last of the lot of three inclosed eggs described in this paper, and the same fate immediately overtook the hen that laid the two inclosed eggs described by Fritsch ('95). Evidently the laying of such eggs indicates a more serious state of affairs so far as the hen is concerned than the laying of double-yolk eggs and brings out again a difference between the ovarian and the oviducal factors.

[1] Inclosed eggs have been recorded as laid in winter (Chobaut, '97), December (Philippi, '93), January (Parona e Grassi, '77), March (Collin, '94; Féré, :02), and at Easter (Schumacher, '96).

As a result of the action of these two factors, three classes of double eggs can be distinguished: first, those whose yolks have come from an abnormal ovary but have passed through a normal oviduct; secondly, those whose yolks have come from a normal ovary but have passed through an abnormal oviduct; and finally, those produced by an ovary and oviduct both of which have been abnormal in their action.

Of the first class little need be said. Although eggs with three yolks are extremely rare, those with two are of rather common occurrence and, as has been pointed out, they are often repeatedly laid by a given hen without injury to herself. As Immermann ('99, p. 10) rightly observed, these eggs fall into two subclasses: the first includes eggs in which the yolks have separate vitelline membranes, and the second those in which the two yolks are within one membrane. In the former the yolks were probably discharged simultaneously from separate ovarian follicles; in the latter both yolks very likely came from the same follicle. When these eggs are incubated, the two embryos begin their development together and proceed at about the same rate. In this respect they are in strong contrast with most inclosed eggs in which, as in the egg described by Féré (:02, p. 349), the inclosed yolk is in advance of the inclosing one in development. The two yolks of double-yolk eggs are usually each of normal size and in consequence induce the formation of a large egg, though the volume of the whole is usually not more than once and a half to once and three quarters that of a normal egg. The fact that hens can lay such large eggs repeatedly and yet without injury to themselves, shows that the death of the hen, which often follows the laying of inclosed eggs, cannot be attributed merely to mechanical causes.

Under this first class of abnormalities have also been placed eggs with yolks of unusual form, such as the apparently double-yolk egg described by Möbius ('95). Since such apparently double or partly double yolks often arise from a rupture of the vitelline membrane and a flowing out of yolk substance, they cannot of course be regarded as real examples of double yolks. Such yolk hernias may be due either to a weak vitelline membrane or, as Davaine ('61, p. 256) has suggested, to a constricted oviduct, but in either case they are not to be classed with true double eggs.

The second class of abnormal eggs includes those in which a normal yolk is received by an abnormal oviduct and in consequence becomes covered with an abnormal set of envelopes. This is represented by eggs that are normal as to contents, form, and size, but are contained in other larger eggs. Instances of this kind have been described by Barnes ('63; '85), Fritsch ('95), Chobaut ('97), and Gruvel (:01). Very likely the second egg described by Supino ('97) belongs to this class, but the inclosed egg, though of normal size, is said to contain an unusual yolk, indicating possibly an ovarian abnormality. Here also should probably be placed an egg recorded by Féré (:02) in which the inclosed yolk, though apparently normal, is contained in a small amount of albumen and what appears to be a thick egg membrane, but is without a shell.

In most of the instances just cited, the enveloping eggs are of two kinds. The first consists of shell, membrane, and albumen as in the cases described by Fritsch, Chobaut, and Gruvel; and the second possesses a yolk in addition to these parts, as in the eggs recorded by Barnes and Supino. The exact method by which a normal egg becomes inclosed in a second more or less complete egg is not wholly clear; but a discussion of this question will be deferred till the third class of eggs has been described.

In the third class of double eggs there is evidence of both ovarian and oviducal abnormalities. In examples of this kind the inclosed eggs usually consist of shell and membrane containing a mass of albumen and a small yolk, as in the cases recorded by Vaillant ('75), Parona e Grassi ('77), de Man ('78), Philippi ('93), Schumacher ('96), Herrick ('99a; '99b, p. 409), and Kunstler et Brascassat (:01); or inclosing albumen but without a yolk, as in the first egg described by Supino ('97), and those described by Herrick ('99b, p. 410), and Gruvel (:02). In this class two types of inclosing eggs might be expected: one with a yolk and one without a yolk, but, strange to say, of the nine instances[1] in which the descriptions are sufficiently full to allow this point to be ascertained, the inclosing egg always consisted of shell, albumen, and yolk.

[1] Parona e Grassi ('77), de Man ('78), Philippi ('93), Schumacher ('96), Supino, two eggs ('97), Herrick, two eggs ('99a; '99b), and Kunstler et Brascassat (:02).

Notwithstanding the fragmentary character of the second egg described in this paper, it undoubtedly falls under the third class; and I am also of the opinion that the three eggs from Mr. Nielson's hen likewise belong here. It will be remembered, however, that of these three eggs the one that was opened presented the remarkable feature, not hitherto recorded to my knowledge, of the absence of yolks from both the inclosed and the inclosing egg, though traces of yolk substance were found in the latter. These traces lead me to believe that the inclosing egg originally contained a yolk which, however, probably broke and almost entirely ran out before the membrane and shell of this egg were formed.

To explain how such inclosed eggs reach their positions, at least two hypotheses have been put forward. According to the first of these, which has been advocated by Davaine ('61, p. 238), Schumacher ('96, p. 368), Herrick ('99b, p. 413), and Kunstler et Brascassat (:01; :02), an egg after having passed by peristalsis to the distal end of the oviduct and after having received its usual coverings of albumen, shell membrane, and shell, is supposed to be carried by antiperistalsis up the oviduct where it meets a second egg, and passing down with this, becomes covered by a second shell, and is laid.

According to the second hypothesis, which has been advanced by Panum ('60, p. 185), Chobaut ('97), and Rabaud (:02), antiperistalsis plays no part in the formation of inclosed eggs, but the egg which is to be inclosed remains in the distal part of the oviduct instead of being laid and is there overtaken by a second egg while the second one is still without shell. After the second egg has enveloped the first, a shell inclosing both is laid down.

In testing these two hypotheses, the chief question is whether or not there is any evidence for antiperistalsis. The common occurrence of a small egg with a limy shell in the albumen of a large one whose shell membrane is intact, seems to me inexplicable except on the assumption of antiperistalsis. Such an egg as the smaller one could not receive its shell except by resting some time in the distal part of the oviduct and it could not come to lie in the albumen of another egg whose shell membrane was not ruptured except by passing to a region in the oviduct above that in which the shell membrane is formed; as this region is proximal to the

shell-forming portion of the duct the operation seems to me to necessitate antiperistalsis. It might be assumed that the inclosed egg made its way into the albumen of the inclosing one by rupturing the shell membrane of the latter just as that egg reached the shell chamber of the oviduct. But there is no evidence in such eggs of a ruptured membrane as this hypothesis would require and indeed there is a case on record (Gruvel, :02, p. 73) in which the inclosed egg apparently met the inclosing one when the shell membranes of the latter were forming and, instead of rupturing them, the inclosed egg remained between the inner and outer membrane and never entered the albumen of the inclosing egg at all. I therefore do not believe that the inclosed egg enters the albumen by rupturing egg membranes but by meeting the inclosing egg by antiperistalsis high in the oviduct and before the membranes have been formed.

Another fact that seems to me impossible of explanation except on the assumption of antiperistalsis is the occurrence of "soft-shelled" eggs in the body-cavities of fowls. This has been recorded by Davaine ('61, p. 241) and more recently by Landois ('99, p. 52), who states that in one instance he found four such eggs in the body-cavity of a hen. Two of these were broken, but two were whole and had all the appearances of normal eggs except that they lacked shells. As there is no source for the albumen and shell membranes of these eggs except the middle and lower part of the oviduct and no way into the body-cavity except by the infundibulum, I believe the conclusion inevitable that these eggs, after the formation of their shell membranes, were moved proximally by antiperistalsis.

How antiperistalsis is excited in the oviducts is not understood. It has been suggested that an egg of small volume might induce such a movement and thus be returned to the upper part of the oviduct, but, though this cannot be denied, it must be remembered that, as Landois ('95, p. 32) has shown, small eggs such as are often found in large ones, may be laid by hens. Moreover, as was stated in describing inclosed eggs of the second class, eggs of normal size are often found within the shell membranes of excessively large eggs and must therefore have moved up the oviduct. Hence the small size of an egg cannot be the only cause of antiperistalsis, if in fact it is at all effective in this respect.

Although in the present state of our knowledge it is impossible to assign a cause for the setting-in of antiperistalsis, it seems to be a process that may occur not only once but even twice in the enveloping of a yolk. Davaine ('61, p. 237) quotes a case in which an egg presented the very unusual condition of three separate envelopes instead of two; these were a firm outer shell, a strong shell membrane, and a thin shell membrane, and a second case is given by Landois ('92, p. 34) of an egg of the red-backed shrike (*Lanius collurio* L.) that had three shells one within the other.

So far as I know, the only objection that has been raised against antiperistalsis of the oviduct has come from Rabaud (:02, p. 201), who claims that this process could not bring two eggs *together*, but would simply move them up or down the oviduct. But such an objection is formal rather than otherwise, for it must be evident to anyone who has watched the process as it occurs in the intestines that its local character is such that eggs could easily be made to approach in the oviduct through its means. I therefore dismiss this objection as without weight.

Although I believe antiperistalsis to be an all important factor in the formation of inclosed eggs, it is in all probability sometimes greatly restricted, as is indicated by an egg described by De Toni ('90) and the second of the two described by Supino ('97). In both these eggs the outer surface of the inclosed shell is adherent to the inner surface of the inclosing one; in other words, the albuminous investment of the inclosed egg is imperfect, as though the smaller egg, while resting in the shell chamber of the oviduct, was imperfectly enveloped by the inclosing egg, whose shell on forming adhered to the inner shell where the envelope was incomplete. Thus an inclosed egg might be imagined to arise after the manner suggested by the second hypothesis already given. But in both these instances the inclosed egg lies in the albumen of the inclosing one and within its shell membrane, and, as already pointed out, it is impossible to explain this position except on the assumption of at least some slight antiperistalsis. I therefore believe that the formation of inclosed eggs cannot take place simply by the undue retention of one egg till it is overtaken by another, as stated in the second hypothesis, but that in all instances some antiperistalsis occurs.

Admitting antiperistalsis to be essential to the formation of inclosed eggs, it is interesting to observe that, notwithstanding the migrations of these eggs, they appear to retain always the same axial relations to the oviduct that they had in the beginning. This is clearly seen in the eggs described by Barnes ('63), Chobaut ('97), Herrick ('99b, p. 410), Kunstler et Brascassat (:02), and Gruvel (:02), as well as in one of those described in this paper, in all of which the point of the inclosed egg is in the direction of that of the inclosing one and not toward its butt, showing that the smaller egg has retained its original axial relations to the oviduct even though it has moved in both directions through that tube. Moreover, when the inclosed egg is so small that it might lie either near the point or near the butt of the inclosing egg, it does as a matter of fact (Barnes, '63; Herrick, '99b, p. 410; Gruvel, :02; and Kunstler et Brascassat, :02) always lie near the point, showing, since the egg moves through the oviduct point forward, that it is the second egg that incloses the first and not the reverse.

In one respect the egg obtained from Mr. Nielson is of special interest. As I have already stated, it contained no yolk in either the inclosed or the inclosing albumen, though traces of yolk substance occurred in the latter near the butt of the inclosed egg. This was due, I believe, to a ruptured and partially escaped yolk. If this explanation is true, is it possible that the yolkless condition of the inclosed egg is also due to the loss of its yolk? It seems well established, however, that albumen can be formed in the oviduct without the presence of a yolk. Possibly foreign bodies when introduced into the oviduct by accident may induce the production of this material. Von Nathusius ('95, p. 655) has pointed out that when a hen lays an egg, the distal portion of the oviduct is so far rolled out that foreign bodies may adhere to it and thus be carried well into its cavity. In this way chicken-yard refuse and feathers, such as have been noted by Landois ('82, p. 23) in eggs, have doubtless reached that position in the oviduct where incorporation in a forming egg was possible. These and like bodies may excite the oviduct to the production of albumen and thus give rise to a core around which a shell might be secreted.

Parasites are also known to make their way into the oviduct, and, though what have been supposed to be tapeworms in eggs

have in all cases thus far carefully inquired into proved to be mere clots of albumen or other like materials (Landois, '94), it is well known that distomes and threadworms do sometimes occur imbedded in egg shells (Landois, '78; Collin, '94). One of these might well form a nucleus around which albumen could be deposited.

But it must also be kept in mind that the ovary and the oviduct are not such independent organs as perhaps has been implied. Davaine ('61, p. 256) states that Claude Bernard opened a hen that had died after laying numerous small yolkless eggs and found the infundibulum closed and the body-cavity full of yolks. It is therefore probable that the simple activity of the ovary may in some indirect way excite the production of albumen in the oviduct, and it is my opinion that many yolkless eggs such as that described in this paper, are formed in this way rather than that they once possessed yolks and through some accident lost them. Such questions, however, are subjects for experimental investigation rather than for speculation.

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BIOLOGICAL RELATIONS OF CERTAIN CACTI[1]

W. A. CANNON

ESPECIAL interest is attached to the study of the cactus family because it is peculiarly well adapted by habit and by structure to withstand the trying conditions of the desert. The greatest development of the group occurs in the arid portions of tropical and subtropical America, but the conception which this statement is likely to give that the cacti thrive best with a modicum of water and live in localities that are too severe for all other desert plants to endure, is erroneous. The cacti like other plants of the desert are most vigorous when the water supply is adequate, and it is by no means certain that such a form as the giant cactus (*Cereus giganteus*) or the barrel cactus (*Echinocactus wislizeni*), as well as the larger Opuntias, do not require a larger amount of water than many of the large plants of other families.

However, it is also likely that no desert plants can live and perpetuate their kind under more arid conditions than some of the cacti. The general means by which they accomplish this are too well known to require repetition here, but certain adaptations to desert conditions, not so well known perhaps, may be pointed out. The most important factor in the life relations of the desert plants is unquestionably the available water supply, and the most striking adaptations accordingly are associated with the absorption, the storage, or the conservation of water. This relation to the water supply, either in apparent independence of it or in intimate association with it, is met at each stage of development. For instance, the seeds of the giant cactus will germinate in summer while lying on the top of air-dry sand and without previous wetting. Seedlings of *Opuntia versicolor* are provided with water-storage organs (Fig. 1) although such are absent in the adult plants. The reaction of the mature plants to a variable water supply is also noteworthy. Specimens of

[1] Papers from the Desert Botanical Laboratory of the Carnegie Institution, No. 11.

Opuntia engelmanni, wrinkled from the loss of water during a long drought (Fig. 2), absorbed sufficient water within two days following a storm to make their joints plump and smooth (Fig. 3). The giant cactus is especially adapted by the peculiar for-

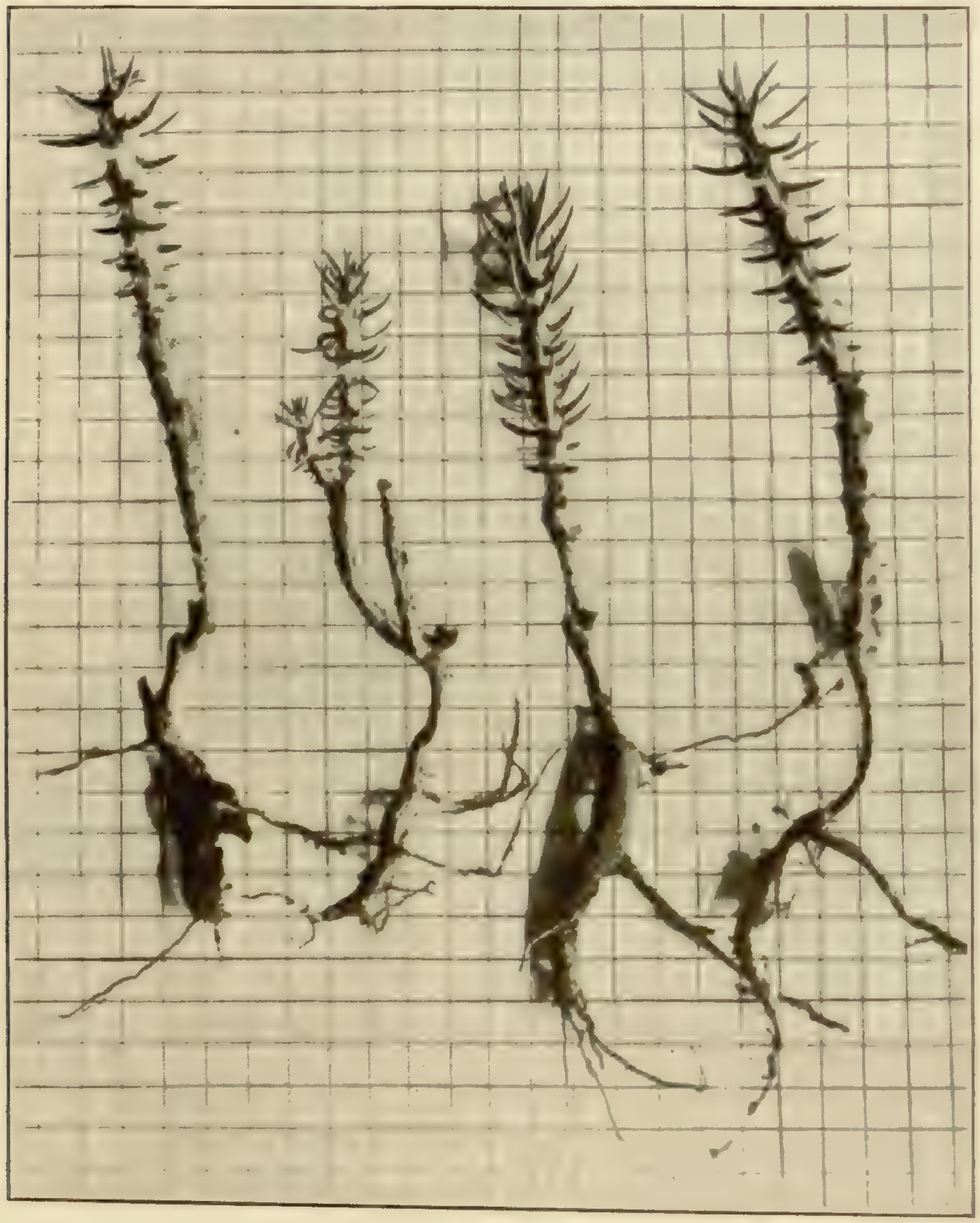

FIG. 1.— Young plants of *Opuntia versicolor* showing the water-storage organs — the swollen roots — which are not present as such in the mature form.

mation of the rind to undergo without injury considerable changes in volume which are induced by a variation in the water content (E. S. Spalding, :05). Other adaptations, such as certain characteristics of the root systems, certain peculiarities of structure and their relation to transpiration, and the transpiration under different conditions may be presented somewhat more fully.

FIG. 2.— *Opuntia engelmanni*, May 11. May 11 marked the close of a severe dry period and the wrinkled surface of the cactus shows that it was suffering from the drought.

THE ROOT SYSTEMS

A special study of the structure and extension of the root systems of desert plants cannot fail to be of great interest and importance in contributing to a right understanding of the biology of these plants. Many characteristics of the desert vegetation are without much question directly traceable to peculiarities of the various root systems. It has been observed (Coville, '93, p. 43) that the fairly equal spacing of desert shrubs is one of the characteristics of their distribution. The primary cause for this is presumably the struggle for water and their distribution is, therefore, an expression of the mutual relationship of the root systems. Again, frequently the form of the root is incompatible with certain habitats,—for example a subirrigated plant would find difficulty in growing where the subsoil is the rock-like *calliche*, —and plants with such deeply penetrating roots, for instance, are for this reason limited in their distribution. It is theoretically possible, and so far as I have observed actually true, that those plants that have a root system which is at once superficial and which penetrates the ground deeply, all other things being equal, may also have the widest choice of habitats. Certain it is that the creosote bush, for example, which has a root system of this character (V. M. Spalding, :04) is perhaps the most widely distributed of our desert shrubs. Although this view of the relation of the character of the root systems to the distribution of these plants is advanced tentatively only, the importance of it as a factor which must be taken into consideration in this connection and sometime carefully studied, is very apparent.

The root system of a specimen of *Echinocactus wislizeni* which was 60 cm. high and 35 cm. in diameter, growing about 75 meters north of the laboratory, was carefully exposed and the course of its roots mapped (Fig. 4). The roots, as the figure indicates, were branched very freely. There were three main roots which arose from the base of the plant not far from 10 cm. from the surface of the ground and which so directed their growth, and that of the branches, that the area compassed by them was about equally apportioned and well covered. As a rule the roots were

FIG. 3.—*Opuntia engelmanni*, May 14. This is the plant shown in Fig. 2. Rains came May 10–12; the plump condition of the joints of the plant on May 14 indicates that water was absorbed promptly after the rains, and in considerable quantity.

slender. At a distance of 15 cm. from the plant one of the largest of them was 7.6 mm. in diameter, and one meter from the plant it was 4.6 mm. in diameter. The roots ran about 6 cm. below the surface, in places which were free of stones, but when a stone was encountered the root dipped beneath it and availed itself of

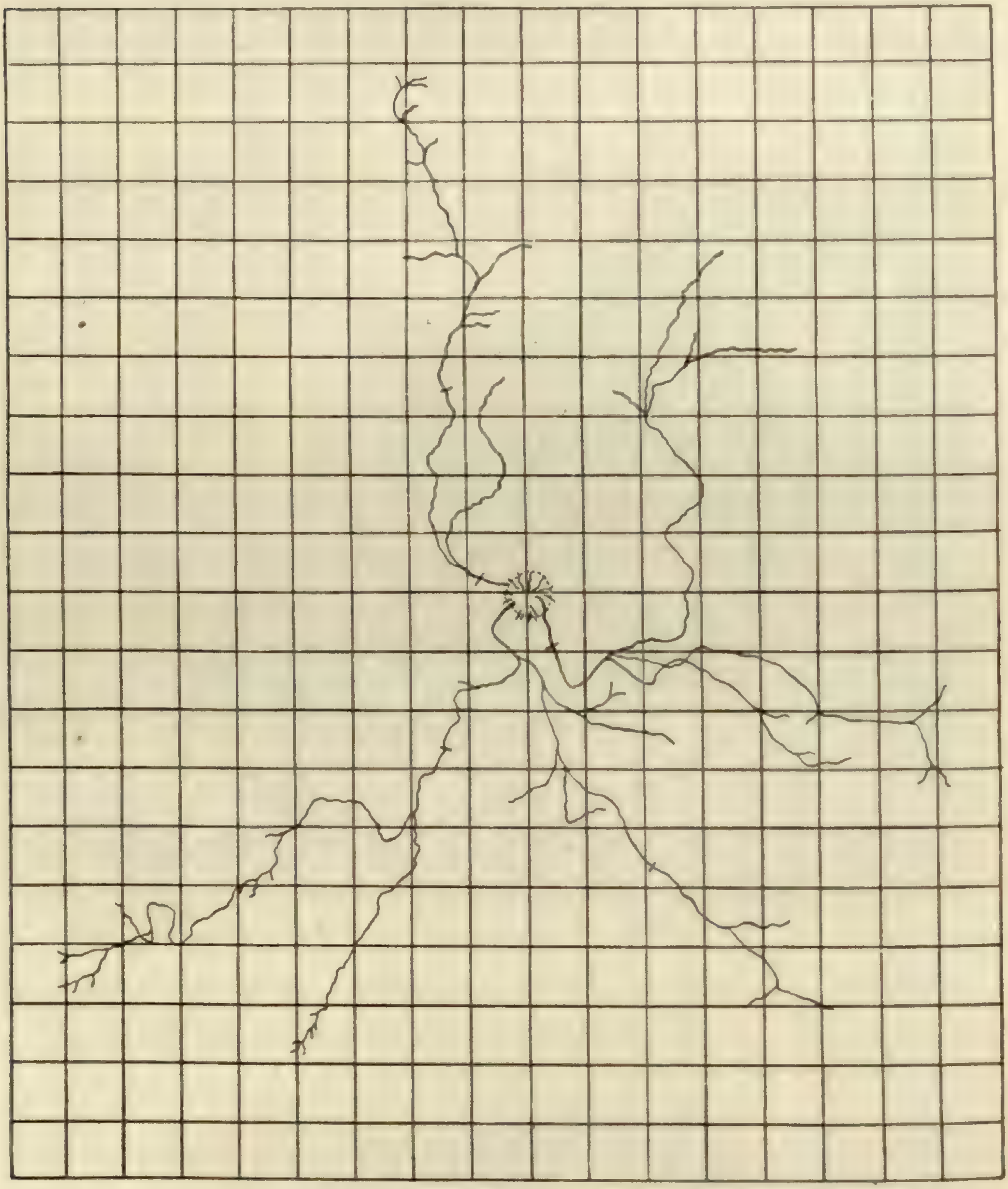

FIG. 4.— Root system of *Echinocactus wislizeni*. Scale: 1 unit = 30 cm.

the better water supply to be found there. The most deeply placed root, however, was not more than 10 cm. below the surface of the ground. There are therefore two noticeable characteristics of the root system of *Echinocactus wislizeni*, namely, the roots

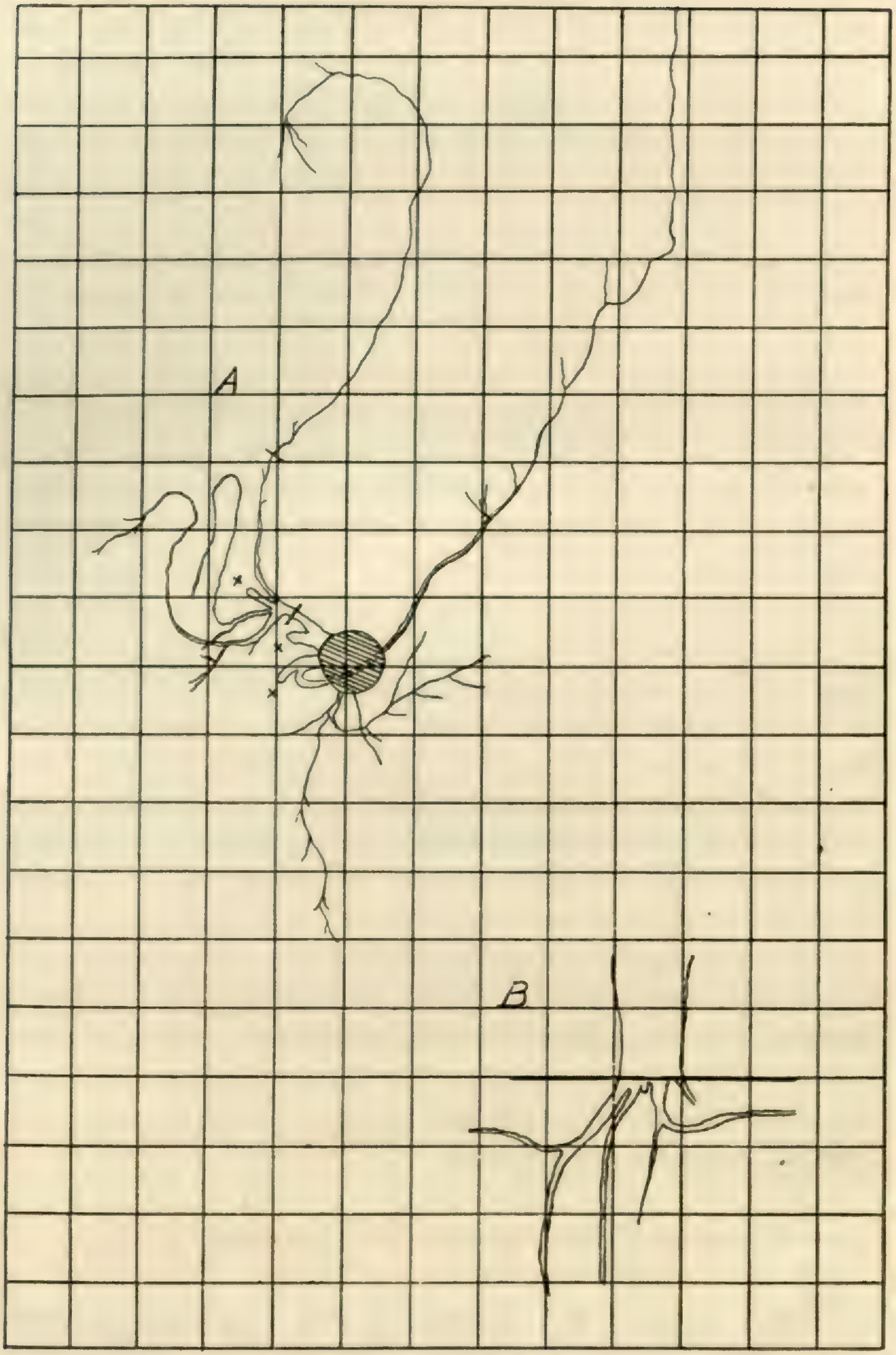

FIG. 5.— Root system of *Cereus giganteus*. Scale: 1 unit = 10 cm.

are slender throughout their entire course and they are superficially placed.

The roots of *Cereus giganteus*, on the other hand, in form and position, and perhaps in extent and branching also, are very different from those of Echinocactus. Fig. 5 represents the root system of a *Cereus giganteus*, about one meter high, which was growing 200 meters west of the Echinocactus just described. Four main roots were observed to arise from the base of the plant. At first they were relatively heavy, from 2 to 4 cm. in diameter at the proximal ends, but they became smaller very rapidly as the distance from the plant increased — in a manner much as is indicated by *A* of the figure. Very soon after leaving the plant the roots branched. One branch, whose later history could not be traced, struck directly downwards, and the other took a more or less horizontal course. The latter branched at intervals, although perhaps not so frequently as those of Echinocactus, and extended, in one instance at least, over one meter from the plant's base. How much farther the root reached could not be learned because of its fragility and the small size of the distal branches. The superficial portion of the root system of *Cereus giganteus* was more deeply placed than were the roots of Echinocactus, and owing to the fact that these parts were not so richly branched, the ground included by them was not so thoroughly covered. However, in one characteristic, which is of interest to note but whose significance I have not investigated, the superficial roots of the two forms are alike, namely, the longer roots and the greatest number of roots are situated on the uphill side of the respective plants. This peculiarity is shown in the two figures. In Fig. 4 the uphill side is to the right, and in Fig. 5 it is at the top of the sketch.

CERTAIN STRUCTURAL FEATURES

Perhaps the correlation of structure and function is nowhere more patent than in the peculiar transpiration-controlling and transpiration-promoting tissues, and the rate of transpiration in certain cacti. As is well known, the cacti are well adapted structurally, laying aside for the moment the matter of water storage,

to retain water for long periods. As an illustration of how long a specimen of *Cereus giganteus* must ordinarily retain water in this locality, the following may be suggested. Calculations based upon the known average water content of these cacti, on the estimated spread of the root system, and on the average rainfall at this place indicate that approximately two years' rainfall, assuming the rainfall to be normal each year, 11.74 in., are required to supply a cactus 15 feet high with an amount of water equal to what it usually contains. The necessity of husbanding the water so hard-gained is even more apparent when the relation of the normal rainfall to the usual evaporation is taken into account. As has been pointed out (Coville and MacDougal, :03, p. 27) the annual evaporation is 7.7 times the rainfall. This is the normal ratio, but when the precipitation is below average, as in 1904 (when it was 75 percent normal) the disparity is even greater (Cannon, :05b).

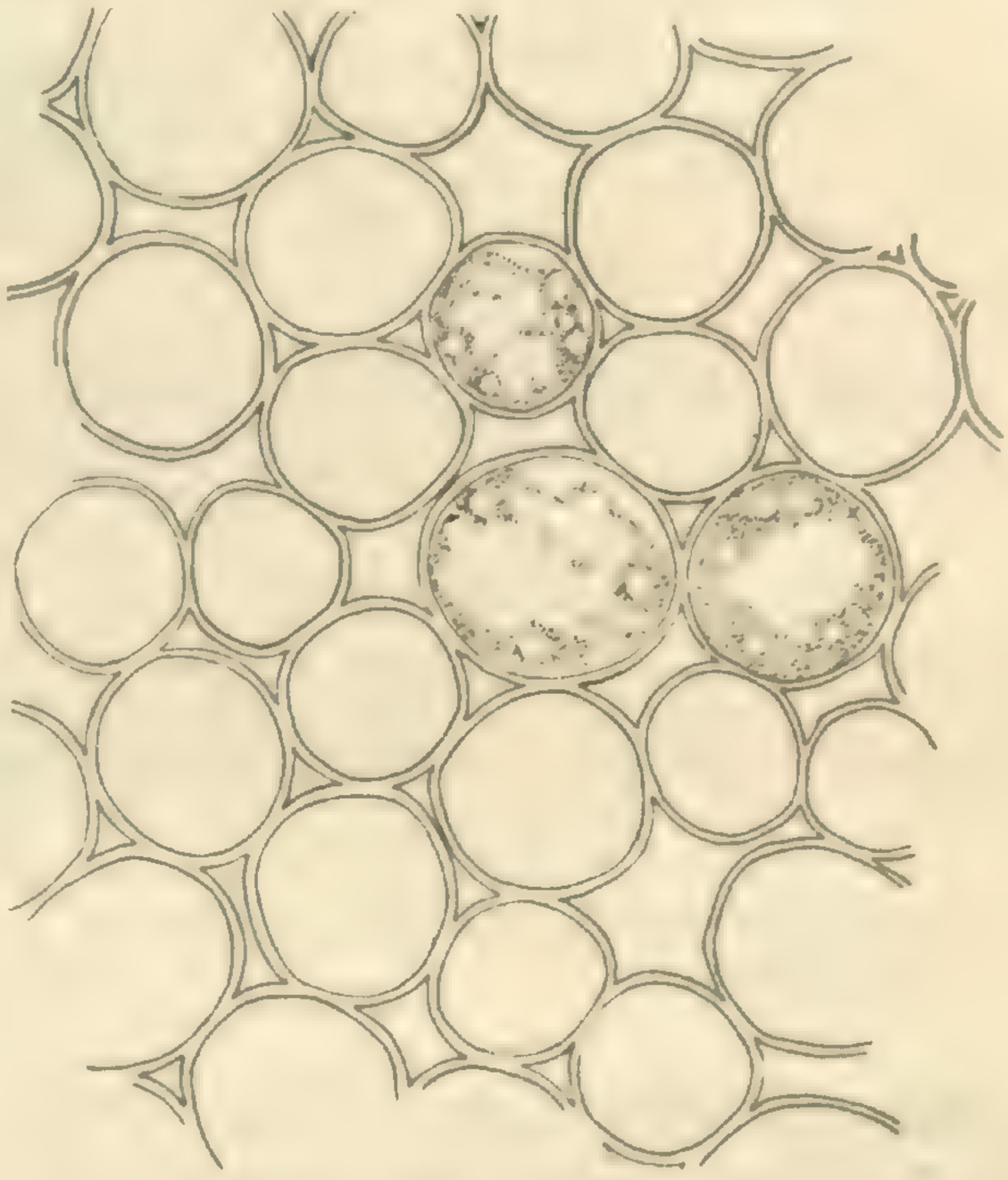

FIG. 6.— *Echinocactus wislizeni*. A portion of the cortex showing chlorenchyma with large intercellular spaces. The section was made parallel to the surface.

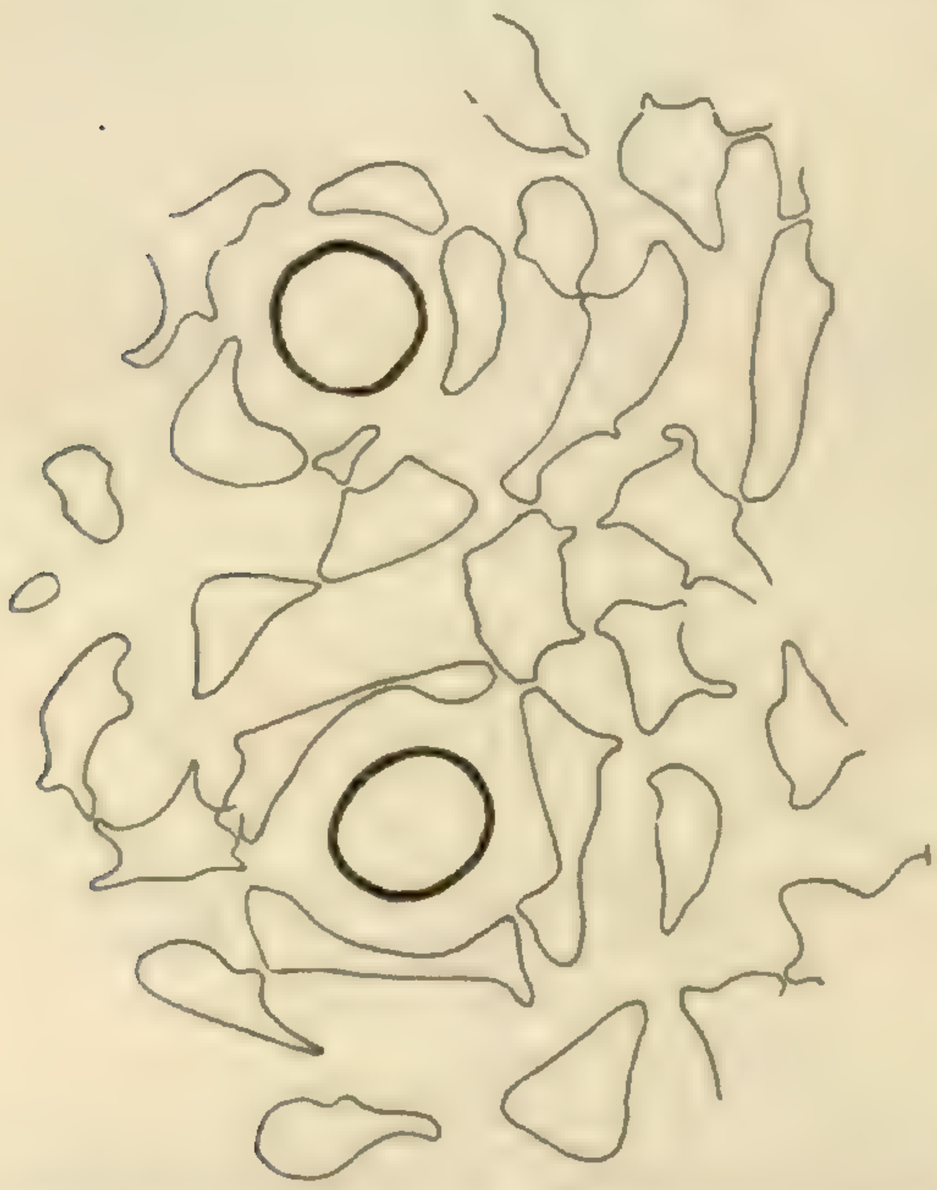

FIG. 7. — *Echinocactus wislizeni*. The heavy-walled supporting tissue lying immediately under the epidermis. This section was parallel to the surface.

Although, as mentioned above, the structural adaptations for the retention of water are well known, reference should here be made to the special adaptations found in *Echinocactus wislizeni*, par-

ticularly on account of the small rate of transpiration which was demonstrated in this plant. Echinocactus has a heavy outer membrane which is cuticularized (Figs. 9, 10). The stomata are peculiarly fitted to guard well a too rapid loss of water, and they have a somewhat complicated structure. The stoma as characteristic of many xerophytic plants, is sunken below the general surface of the stem, and from it in Echinocactus a tube, divisible into two portions of separate function, leads deeply into the outer portion of the cortex and becomes the peripheral portion of the extensive intercellular aërating system of the plant. The substomal tube, really trachea, is shown schematically in Fig. 11. The outer portion, which is heavily shaded in the sketch, is cuticularized throughout its course in the sclerenchymatous tissue (Fig. 10) of the cortex, and in this part it acts merely as a tube for the conduction of gases. Beneath the supporting tissue the tube enters the chlorenchyma and its wall is no longer cuticularized; it here functions as the substomal chamber proper.

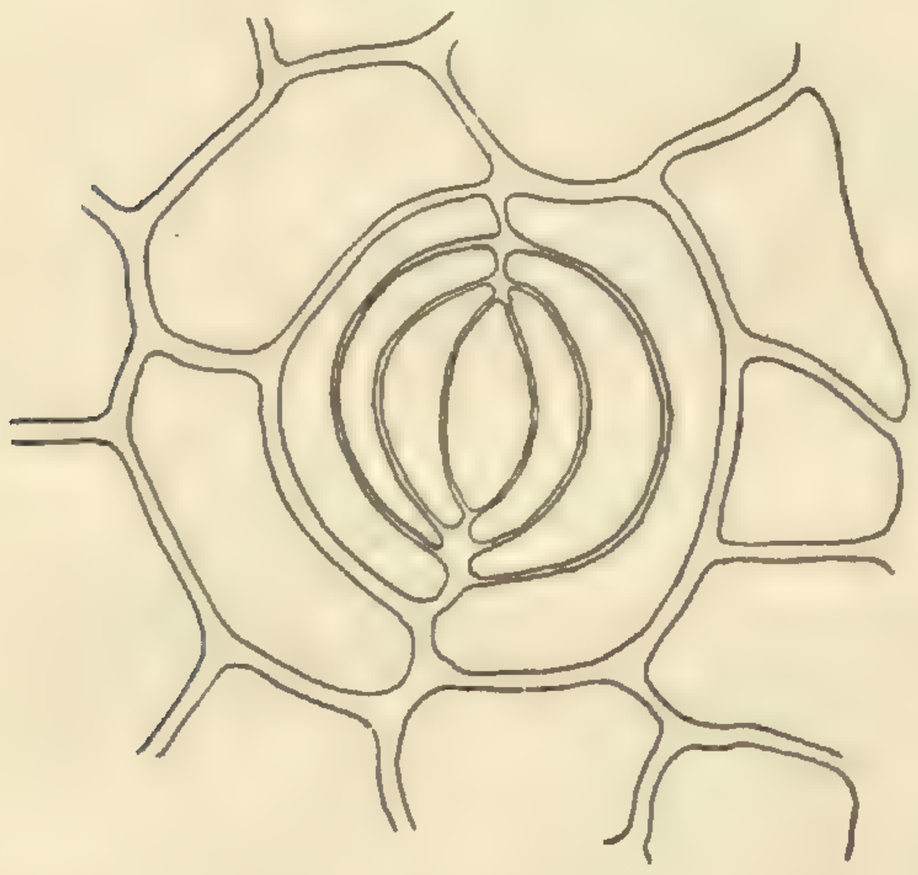

FIG. 8.— *Echinocactus wislizeni*. Surface view of stoma.

It is of interest to contrast with this permanent structure a form of stoma and sort of adjoining tissue which are a part of evanescent organs, and which also appear to have somewhat different functions. I have reference to the stomata of the leaves of *Opuntia versicolor*. The permanent stomata of this Opuntia closely resemble those of Echinocactus but the temporary stomata, those of the leaves, are very

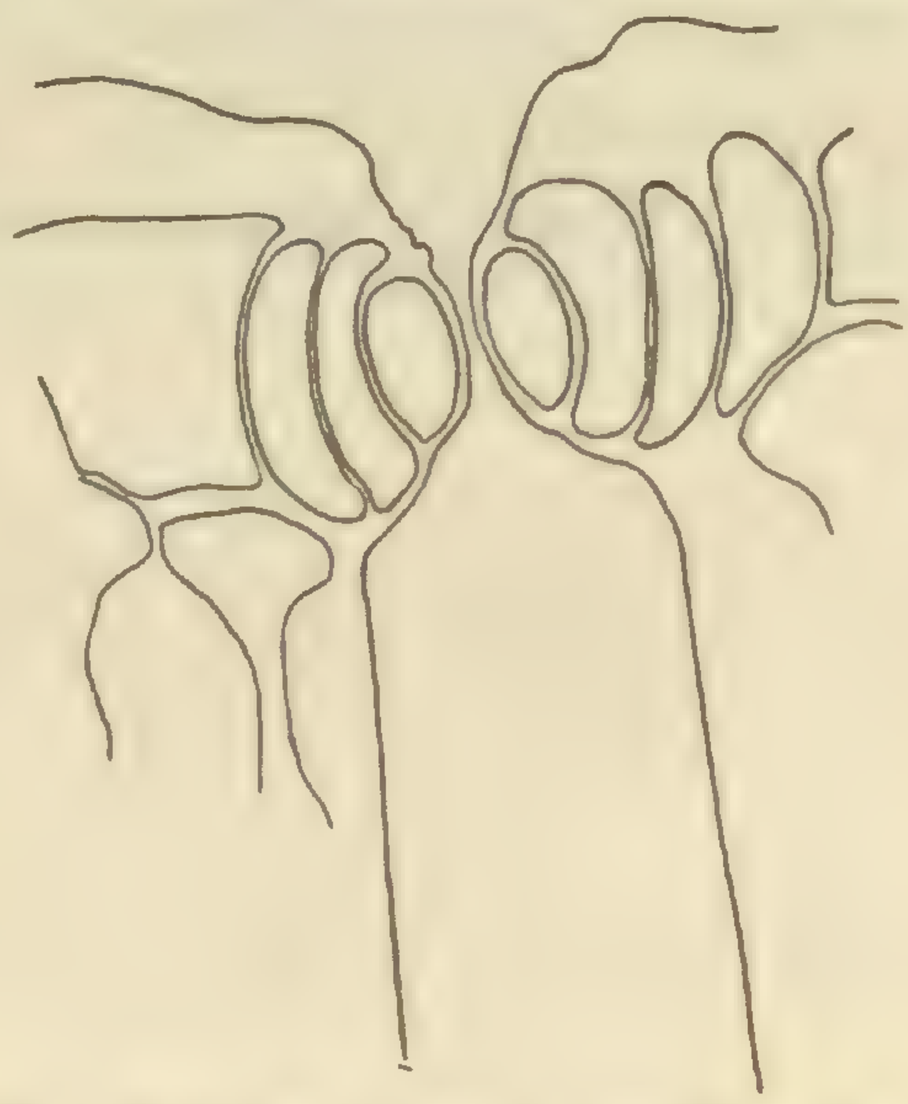

FIG. 9.— *Echinocactus wislizeni*. Stomata and substomal canal which passes through the supporting tissue (see Fig. 7) to the more deeply placed chlorenchyma (Fig. 6).

different (Figs. 12–14). These stomata are superficially placed

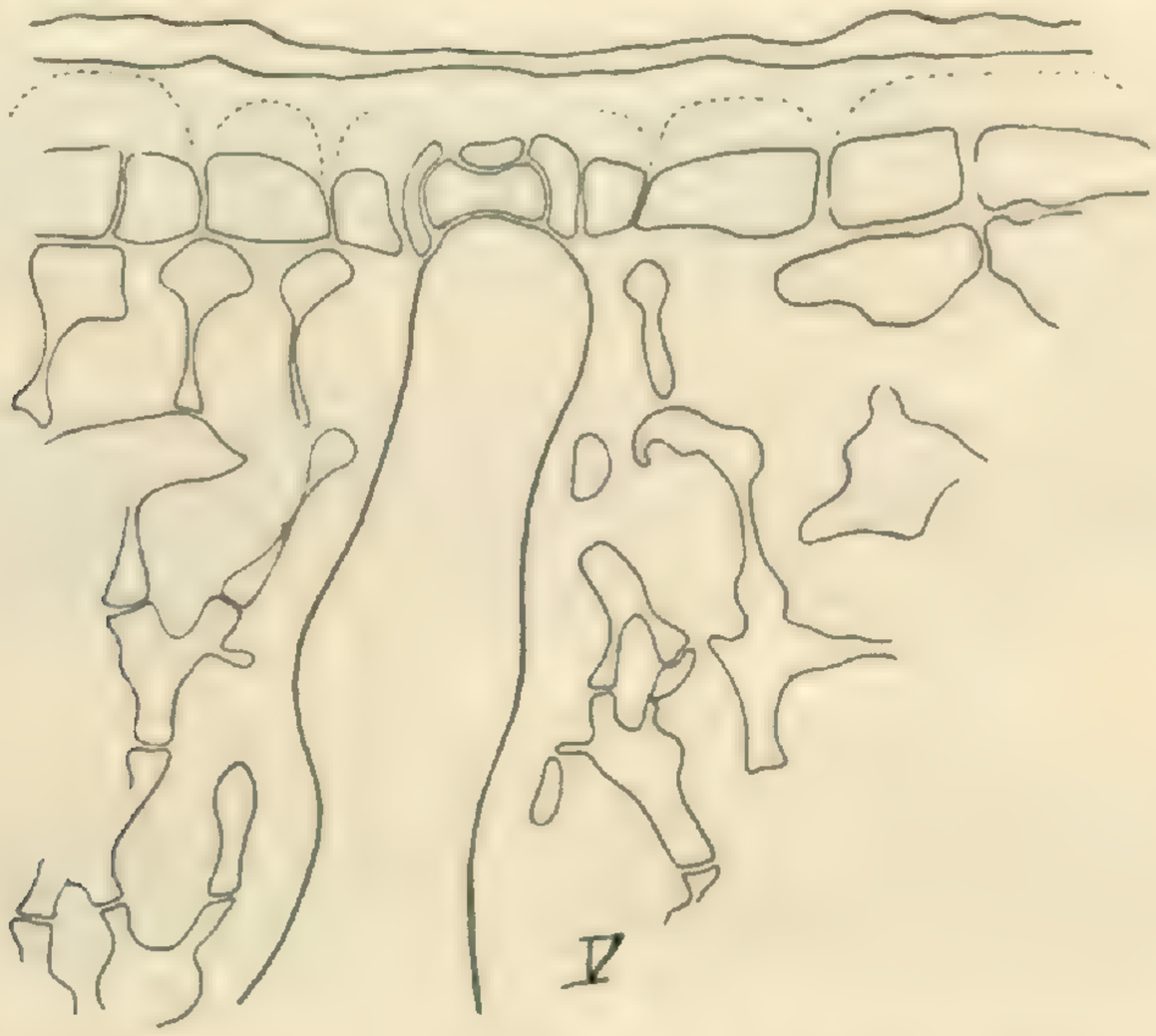

FIG. 10.— *Echinocactus wislizeni*. Same as Fig. 9, to show character of supporting tissue.

and they open directly into the substomal chamber (Fig. 12). The substomal canal of the permanent organ, therefore is lacking. Associated with this form of stoma is the absence of a sclerenchymatous supporting tissue, and, consequently, the extension of the chlorenchyma to the epidermis. The heavy outer epidermal wall of the older portions of Echinocactus is here replaced by a delicate one. In connection with this structure of the leaves of Opuntia appears their function of promoting transpiration, and presumably the respiratory activities as well, and in this they render it an important service, as will be apparent from the results of the transpiration studies.

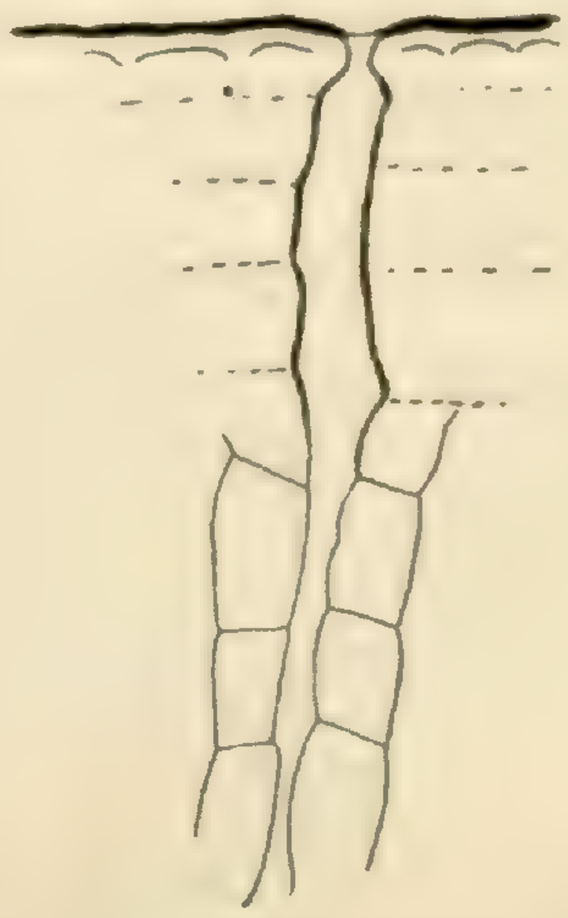

FIG. 11.— *Echinocactus wislizeni*. Semidiagrammatic sketch showing the relations of the substomal canal. That portion of it which is in the supporting tissue is heavily shaded; that portion in the chlorenchyma is represented by a lighter wall.

TRANSPIRATION OF CEREUS AND ECHINOCACTUS

In all of the studies on the transpiration of cacti which were conducted outdoors the polymeter method (Cannon :05a), described elsewhere, was employed. A few, however, which will be pointed

out later, were done in the laboratory by weighing in a manner

Fig. 12.— *Opuntia versicolor*. Cross section of a leaf showing two stomata, one of which was cut in two at right angles to the guard cells and the other parallel to and to one side of them. The confluent substomal chamber is shown. This section is to be contrasted with Fig. 13.

to be described. This change in method was made necessary on account of the high relative humidity prevailing at the time.

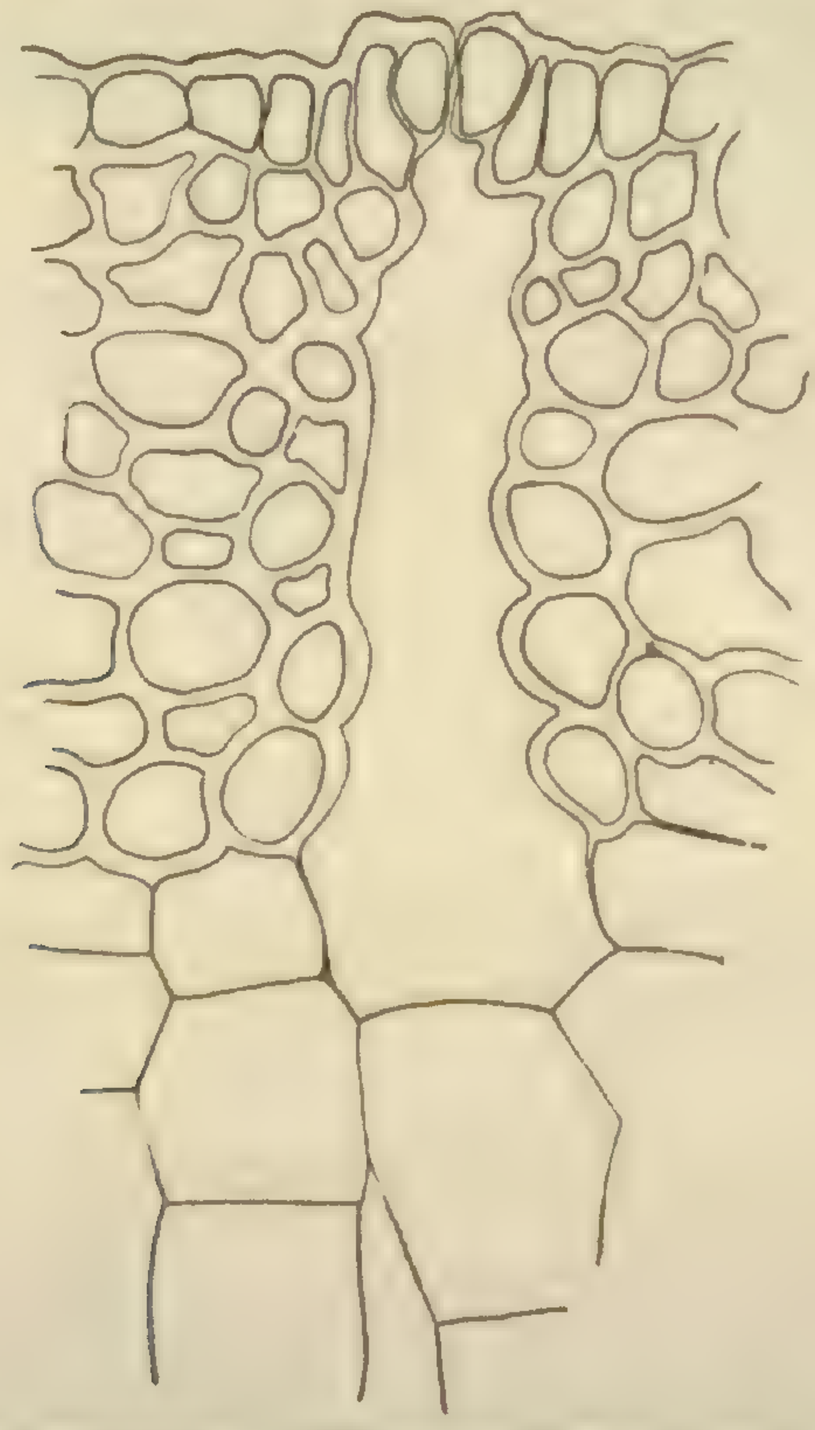

Fig. 13.— *Opuntia versicolor*. Substomal canal and partly developed supporting tissue of a young stem.

Experiment No. 1. Cereus giganteus

Time	Percent of Saturation	Temperature	Amount in Milligrams
9:27 A. M.	42.0	94° F.	67.5[1]
10:37 A. M.	48.5	105° F.	106.0

The cactus was located in the shade of a *palo verde* (*Parkinsonia microphylla*) on a dry mountain-side not far above the bed of Salvino Canyon, 18 miles east of the Laboratory. Higher

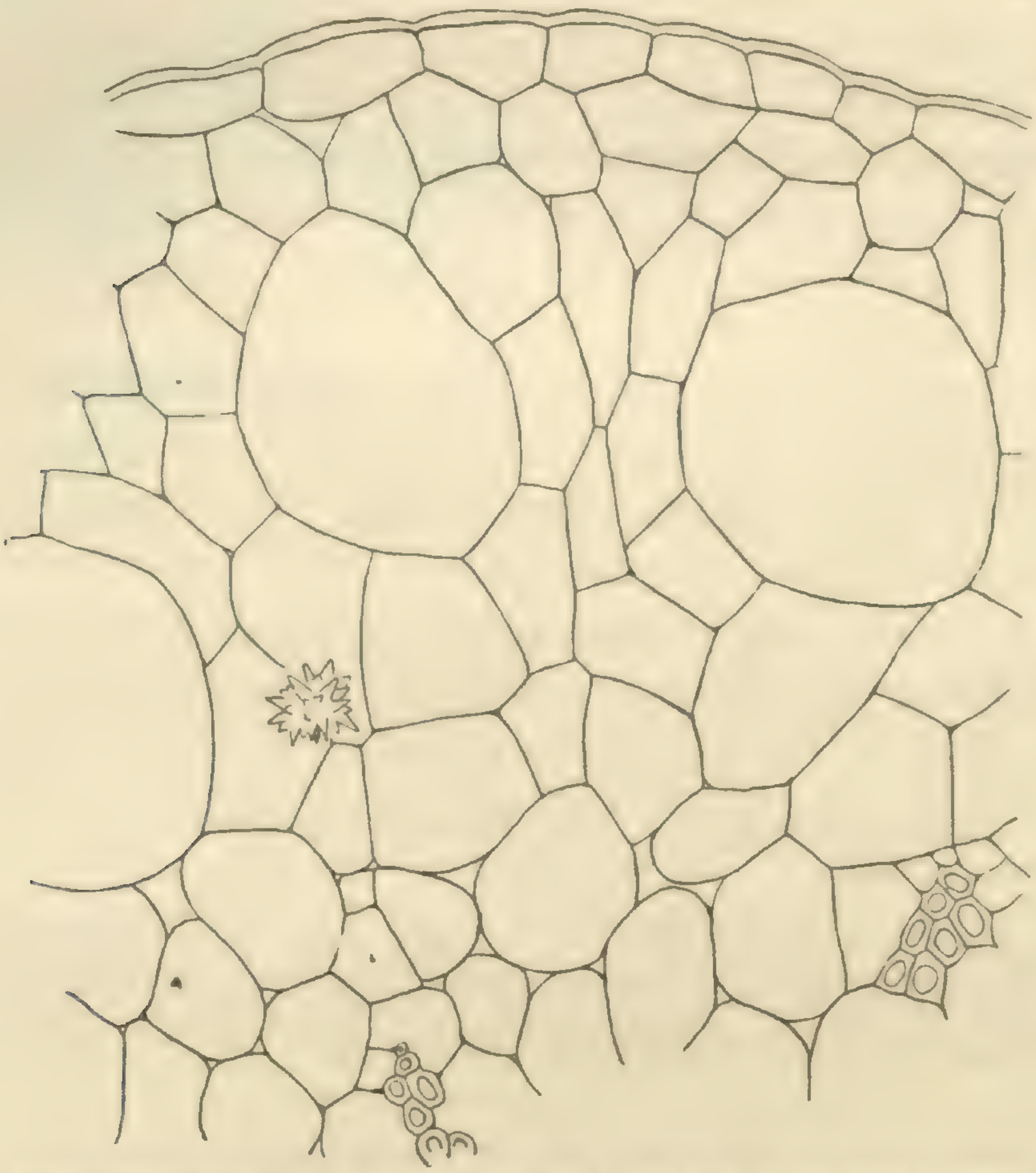

FIG. 14.—*Opuntia versicolor*. Cross section of a leaf to illustrate its delicate structure.

on the same slope were many other giant cacti of large size, and other typical desert plants such as *Encelia farinosa*, *Fouquieria splendens*, as well as other species of cacti.

[1] The first amount in each case is the absolute humidity of the atmosphere of the bell glass when the experiment begins. The second amount is the absolute humidity at the close of the experiment. The difference between the two is the amount transpired.

The transpiration of the cactus was taken September 9, and as the high relative humidity at the beginning of the experiment shows, the effects of the rains of August were still manifest. The rate which is 0.2 milligrams per minute for 100 sq. cm. of transpiring surface, may be considered a high one, since without exception the greatest rate of transpiration of all the plants, whose seasonal variation in rate has been observed, has been after or at the time of the summer rains.

Experiment 2. *Echinocactus wislizeni*

Time	Percent of Saturation	Temperature	Amount in Milligrams
10: 28 A. M.	32.5	82° F.	36.0
2: 05 P. M.	35.5	91° F.	51.0

This experiment took place on March 19, at the Desert Botanical Laboratory.

The rate of transpiration of the entire plant per hour is 3.4 milligrams.

On September 3 the experiment was repeated when the following data were derived:—

Experiment 3. *Echinocactus wislizeni*

Time	Percent of Saturation	Temperature	Amount in Milligrams
12: 24 P. M.	35	104° F.	60
3: 14 P. M.	45	109° F.	89

The rate for the entire plant is 9.6 milligrams per hour.

This specimen of Echinocactus is growing on a westerly slope on the Laboratory Mountain. In its vicinity are found a few giant cacti and *Encelia farinosa*, *Lycium* sp., and *Parkinsonia microphylla*. Because of the desirability of preserving this specimen the surface was not computed and therefore the rate cannot be compared directly with that of *Cereus giganteus* as given in the preceding experiment. However, it happened that the two cacti were of nearly the same size,—10 cm. in height,—and a general comparison between the two can be made. The rate of

Cereus per hour was approximately 33 milligrams while that of Echinocactus on September 3 was 9.6 milligrams. Whether this difference in the rate is constant for the two genera, or is attributable to other and unknown causes aside from the relatively slight difference in surface, is not known.

Transpiration of *Opuntia versicolor*

A specimen of *Opuntia versicolor* about 20 cm. high, growing near the laboratory building, was studied at various times during the dry portions of the year (1904), namely, in March, April, June, and July. The observations indicate that the reaction of Opuntia to water is very different from that of other desert plants, such for instance as *Covillea tridentata*, *Encelia farinosa*, or *Fouquieria splendens* (Cannon, :05a, p. 404), suggesting a unique position among its associates and an important factor among the varied ones that brought about the present distribution of the group to which it belongs.

As has been shown in another place, the transpiration of *Fouquieria splendens*, as well as that of other desert plants and plants of more humid regions (Burgerstein, :04), under certain conditions increases with an addition to the available water supply (see Cannon, :05b; V. M. Spalding, :04, :05). Thus after rains, but before leaves appeared, the rate of transpiration of *Fouquieria splendens* increased about three fold; after leaves had been formed and while they were developing the rate was relatively very great. A similar condition was likewise observed in *Encelia farinosa*, *Covillea tridentata*, and in other plants. In *Opuntia versicolor*, however (see Figs. 2, 3), and probably in other Opuntias the response to the rains is indeed also positive but in a very different way. The cactus absorbs water greedily, and as a consequence it at once increases in size, and its tissues become turgid. But, so far as I observed, the rate of transpiration did not increase proportionally. Indeed, laboratory experiments, in which a small specimen of *O. versicolor* was attached to a potometer by a long delicate tube so that the cactus could be weighed at intervals at the same time that its rate of absorption was being recorded, showed very clearly that under such

conditions the cactus may absorb water much faster than it gives it up by transpiration.

It should be noted that the specimens of cactus which were experimented upon both in the field and in the laboratory did not have an adequate water supply at their disposal previous to the times of the experiments. As a general thing not until some time has passed after the water has been absorbed, does new growth appear with its embryonic structure and its evanescent leaves and then only does the rate of transpiration become greatly increased. During the periods of drought the plants make but little new tissue. These peculiarities of *Opuntia versicolor* were observed repeatedly and will be presented in the succeeding *résumé* of representative experiments.

The transpiration of *Opuntia versicolor*,—an entire plant,—was as follows:—

March 25	. . . .	51.0	milligrams	in one hour
March 26	. . . .	63.0[1]	"	" " "
April 25	. . . .	19.9	"	" " "
June 30	. . . .	27.5	"	" " "
July 4	. . . .	26.1	"	" " "

During the period from March to July the rainfall was unusually small and the cactus had an insufficient supply of water. The rates of March, April, and June, therefore, represent the transpiratory activities of the plant in times of drought. At various times in the midst of the dry seasons Fouquieria, Covillea, and other plants had been irrigated and the effects on their transpiration were recorded (Cannon, :05b). To learn how an increase in the water supply of *Opuntia versicolor* would influence its rate, as well as to learn how the rate under such circumstances would compare with that during dry conditions, it, also, was irrigated. On June 27, which was a time of drought, nine gallons of water were poured slowly on the ground at the base of the cactus, but it did not show by an accelerated rate (see the rate of July 4, above) that it had absorbed any of the water. That it had really done so, however, was indicated by the fact that the plant had become rigid by the increased turgescence of its tissues.

[1] Unfortunately a small branch was broken from the plant after this experiment so that the winter and the summer rates are not comparable.

The transpiring surface of the Opuntia was not estimated, so that its rate cannot be compared directly with the rate of other cacti or plants of other families although this, perhaps, is of minor consequence. The important fact was established that the plant does transpire measurable amounts of water even in the driest times and that it absorbs water quite out of proportion to its rate of transpiration.

I wish now to call attention to a phase of the biology of *Opuntia versicolor* which is also of great importance in the economy of the plant but which has hitherto received little emphasis, namely, to the *rôle* which the leaves play in transpiration.

On August 18 the polymeter apparatus (Cannon, :05a, Fig. 4) was adjusted to take the transpiration of a branch of the cactus which bore leaves and which was situated a few meters north of the laboratory building. The data derived from this experiment are as follows:—

Experiment 4. *Transpiration of Leaves of Opuntia versicolor*

Time	Percent of Saturation	Temperature	Amount in Milligrams
2:20 P. M.	40	95° F.	62.
2:30 P. M.	59	98° F.	101.

The branch transpired at the rate of 234 milligrams in one hour, or 0.91 milligrams per minute for 100 sq. cm. of transpiring surface.

As soon as the experiment was finished the surface to the stem was coated with vaseline and the experiment was repeated. The following, therefore, is the transpiration of the leaves only.

Time	Percent of Saturation	Temperature	Amount in Milligrams
2:42 P. M.	41.5	97° F.	69.
2:52 P. M.	52.0	100° F.	87.

The rate per hour for the leaves of the branch is 108 milligrams, or 0.42 milligrams a minute for 100 sq. cm. of surface.

The surface of the stem alone was estimated at 331 sq. cm.; that of the leaves at 97 sq. cm. Therefore with somewhat less

than one fourth the entire transpiring surface, the leaves alone transpired nearly one half the whole amount.

The high humidity at this time was unfavorable to the further use of the polymeter method so that the experiments upon the transpiration of the leaves of the cactus were continued with a special weighing apparatus in its stead. Since the results of all of these experiments were essentially alike, I shall refer to one of them only.

A branch of *Opuntia versicolor* with leaves was placed in a bottle containing water which was so arranged, with a capillary tube as well as the branch fastened in the stopper, that the air could enter and maintain a pressure within uniform with that of the room, while only an inappreciable quantity of vapor escaped. In one hour, 2 : 15 to 3 : 15 P. M., the branch lost 180 milligrams in weight. The stem was then coated with vaseline and in one hour, 3 : 30 to 4 : 30 P. M., the loss of weight was 100 milligrams, which was, of course, the transpiration of the leaves only.

There were 69 leaves on the branch whose entire surface was estimated at 55 sq. cm. The surface of the stem alone was 65 sq. cm. Therefore the leaves had about 45 percent of the entire transpiring surface and they gave off about 55 percent of the entire amount transpired.

SUMMARY AND CONCLUSIONS

The leading points in this paper and the conclusions may be briefly stated in the following summary.

1. The root systems of *Cereus giganteus* and of *Echinocactus wislizeni* which were studied and mapped, present characteristic differences. The root system of Cereus is in part superficial and in part deeply placed. The root system of Echinocactus is superficial only. There appears to be a relation between the character of the root systems of these plants and that of the habitats in which they naturally occur. For example, the form and the extension of the roots of Cereus inhibit its occurrence in localities where the underlying formation is of such nature that they cannot reach the usual or needful depth. We accordingly find the plant on rocky mountains, or where the soil is deep, but in this locality

it does not grow at all, or rarely, on the *mesa* where the rock-like *calliche* forms a thick and nearly impenetrable stratum which reaches almost to the surface. However, it may not be wholly a problem of anchorage, since the morphological condition may be associated with a physiological one, as for instance, subirrigation or proper drainage which may be indispensable factors in its water relations. Although the character of the root system may thus be closely connected with the character of the habitat, certain features in the local distribution indicate that it cannot be too narrowly insisted upon. For example, *Cereus giganteus* avoids northern slopes, although to all outward appearances the structure and the water supply may be quite the same as on the other sides.

Echinocactus presents quite a different condition of affairs. The plant does not require unusual protection against lateral stresses. It grows most abundantly in this locality on the *mesa* where the soil is shallow. The roots are so placed that they can neither afford safe anchorage for a tall plant, nor absorb water at the water level. There is therefore a direct relation between the character of the plant and that of the root system, on the one hand, and the character of the root system and that of the habitat, on the other. It should also be noted that the roots of Echinocactus, which are very shallowly placed, permit the plant to derive benefit from relatively small rains, but, by the same token, that they prevent it from getting water other than what falls on the area included by them.

2. The striking disproportion between absorption and transpiration, which was observed in *Opuntia versicolor*, is thought to be of great importance in accounting for the distribution of the plant (and perhaps of the family) in those parts where evaporation greatly exceeds precipitation.

3. A low rate of transpiration was demonstrated in *Opuntia versicolor* and *Echinocactus wislizeni* during periods of prolonged drought. At the time of the summer rains the rate was greatly increased and in all instances the increase was associated with the renewal of growth.

4. A direct relation was observed between structure and transpiration. The mature portions of Echinocactus and of *Opuntia*

versicolor are suited by the heavy outer epidermal wall, which is cuticularized, as well as by the stomata of peculiar structure, to resist rapid loss of water. This is the type of structure that is to be found during the periods of drought. The embryonic portions of these cacti, and the evanescent organs, in which are included the leaves of Opuntia, are well adapted to promote transpiration. This is accomplished in the embryonic tissues by a thin epidermal wall and by the undifferentiated portions of the outer part of the cortex by which a rapid transfer of water is possible. The substomal tube functions also throughout its entire length as the substomal chamber. In the leaves of Opuntia not only is the epidermal wall delicate, but the outer cortex is never differentiated into sclerenchyma and chlorenchyma and there is no substomal canal. Such is the structure of the tissues at the times when the rate of transpiration is most active.

5. The leaves of *Opuntia versicolor* play an important *rôle* in transpiration. In one instance with somewhat less than one fourth the entire transpiring surface the leaves transpired nearly one half the whole amount. In another instance about 45 percent of the entire transpiring surface was foliar and the leaves transpired about 55 percent of the total amount.

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CONTRIBUTIONS TO THE PHYSIOLOGY AND BIOLOGY OF THE DUGONG

H. DEXLER AND L. FREUND

The accounts of the habits of the dugong that have hitherto been brought to the notice of naturalists are really limited to a detailed description by Klunzinger, who as surgeon on the "*Koseir*" in the sixties, collected these accounts of the dugong of the Red Sea from the Bedouins. The account in Brehm's *Tierleben* is taken from him. The few who before or after him have had to do with the subject, have added but little that was new. For this reason we are warranted in publishing some very recent observations based on the field notes of one of us (Dexler). In 1901, through the generous support of the Gesellschaft zur Förderung deutscher Wissenschaft, Kunst, und Literatur in Böhmen, Dexler was enabled to make a visit of several months to the Coral Sea, and there to attend personally to the capture of the dugong. Incidentally, also, the rare opportunity was afforded of observing minutely for forty-eight hours the habits of a captive dugong, and to investigate in life what has hitherto been impossible for us to find out in the case of this animal.

The low flat coast of East Australia is a favorite haunt of the dugong. Here are broad, shallow bays choked with sand and covered with water at low tide, and connected with the outer ocean by numerous channels and passages. Here is the plant-bearing sea bottom on which occur the so called "dugong grasses" that constitute the food of the dugong. These bottoms are the chosen pasture of the dugong and it is one of their permanent occupants, being directly dependent for sustenance upon places of this sort. Wherever there are these conditions, to which must be added sea water and a particular temperature, there the dugong will be found as all observers agree (Ruppel, Klunzinger, Finsch, Semon). Sea water is its native element and it is questionable if it occurs at all in brackish water at the mouths of rivers, as is

maintained by many, *e. g.*, Brown. But as Finsch has stated, observations on this point are lacking, and we ourselves observed nothing of the sort. It is not known by the old Queensland dugong fishers to enter brackish water, and that it seeks the fresh water of the river itself is out of the question.

During the day the dugong remains in the deeper waters of the outer ocean and only at night comes in through the channels previously mentioned to feed in the bay. This observation is corroborated by those of Klunzinger in the Red Sea, and by the statements of Semon and Finsch. With regard to its appearance at night, Klunzinger makes a noteworthy statement based on the accounts of the Bedouins. According to them the dugong is recognized at night not only by its "blow" and by the phosphorescence of the disturbed water, but also, they asserted, by three shining spots on the back, a fact of which he was repeatedly assured but which he found it difficult to believe. Krauss attributed this to the luminosity of the sea, but by Brehm it is explained as due to the sparkling in three places of the water that is disturbed in swimming, and thus made luminous. These three places would correspond well to the rounded ripples that would be made by the head, the middle of the back, and the caudal fin. Langkavel also cites Klunzinger's statement. No such phenomenon was observed in the Australian waters, a fact that may have been in part due to the slight degree of phosphorescence of the surface water at that time of the year (the Australian winter). However, in spite of the bright light of the tropical sea, it is highly probable that this is a faulty observation, and untrue of the dugong. For as it swims, its head first appears above water to take breath, rarely the back follows, while the tail is never shown. These movements might very well produce a more or less clear flashing when the water is strongly phosphorescent, but it would seem quite as impossible to identify the animal by this as to tell it by the noise it makes in breathing. Dexler hunted the animals in waters inhabited by both dugongs and dolphins, and in the tropical nights made careful observations for many hours while lying in wait at the nets in their pursuit. At no time, however, was it possible to distinguish the two by their resounding "blow" though often they were extremely near at

hand. Moreover, the blackfish hunters were questioned in regard to this point, and although they are extraordinarily expert in whatever has to do with the pursuit of their quarry, they were unable to distinguish between the sounds produced by the breath of these animals.

It is well known that the movements of the dugong in swimming are slow and clumsy (Klunzinger and Finsch). Thus late one evening Dexler observed from his boat, six dugongs that lazily broke water scarcely ten meters away, and with a forward rolling movement disappeared again. As a rule, only the nasal portion of the head came above water in taking breath as Ruppel also has observed ; but Ruppel and Semon likewise agree in stating that very rarely the anterior part of the body or the entire head may appear.

Before proceeding to describe certain peculiarities of biological interest, we may add the important observations made on a captive live dugong that have furnished the basis for the systematic treatment of the biological material to follow. More particular details as to capture will also be given shortly.

On one occasion when the nets were examined, there were found in them a large ray, an ocean-butterfly, and a dugong whose tail had become entangled in the net, though otherwise the animal was able to move freely. This might be called very unusual, for the animals generally strike the net headfirst, or with one of the flippers, getting entangled, and while hanging in the net they thrash and roll about until they are completely entangled by the cords. The heavy net is thus drawn together into a solid mass and the dugong, no longer able to raise it in order to come to the surface for breath, is drowned. In the present case, as the net was tightly drawn together, it could not be pulled up on the spot, and it was decided to drag the whole thing out onto the shore, with the captive in tow. The fast cutter had some difficulty in pulling the animal, but despite its tremendous struggles it was towed along after the boat, tail first in the gurgling wake. Twice the boat was stopped in order to allow the exhausted bull to obtain air, and on these occasions it became very excited and unmanageable. It kept constantly trying to dive, jerking its arched body into the deep, and when it

felt the pull on its tail it rolled over and over on its long axis two or three times. Repeatedly during these movements, it voided gaseous and solid excrement which diffused the characteristic odor of the dugong. The captive came up to breathe at intervals of from 14 to 42 seconds, exhaled with a long and forcible "blow" and inhaled with less noise and more quickly. Then the diving and rolling were repeated.

With the flood tide the boat was brought over the bar to the mouth of the Wallumkreek and there anchored. Here in the shallow water the animal became for the first time somewhat quiet after the people had withdrawn, but when the dingies put off from land again and approached it, straightway the diving and struggling began anew. From this it seemed that it was not so much the sight of the approaching boats as it was the sound that acted upon the animal's consciousness. If a black cloth or a piece of white canvas were waved above its head, the animal was not visibly disturbed or only rarely. But if one stamped on the deck then immediately it thrust its nose into the sand in a reflex diving or escaping movement.

It was a simple matter to secure the dugong, for the helpless animal had hardly more than its great weight with which to oppose its capture. A strong line was soon tied about its tail and made fast to the shore, and the dugong was then rolled out of the net into the water. There it appeared to feel better and began at once to thrash clumsily about, and tried to hide underneath the cutter. However, the strain on the line soon relaxed and with but slight exertion the dugong could be dragged into shallow water. By this time it put its snout above water for breath at intervals of from 17 to 65 seconds and breathed in the manner above described. If anyone spoke, or struck the tiller, or rattled the anchor chain, or made any other noise, the dugong started off violently and tried to dive deeper with a movement like that of the dolphins that roll head foremost over the surface of the water. In these attempts the animal repeatedly struck the sand bottom with considerable force. As soon as the line drew taut and the dugong felt the pull, it at once executed those remarkable rapid revolutions on the long axis of its body so that the line began to crack. When the noise ceased, the dugong soon became quiet and

lay motionless at the bottom, resigned to its fate. The intervals between breaths also became longer; at first they were from 43 to 60 seconds, then later, from 100 to 120 seconds apart. The following intervals were particularly noted: 104, 43, 60, 58, 95, 45, 105, 145, 85, 52, 50, 56, 120, and 85 seconds. The longest interval was 145 seconds though of course it must be kept in mind that in this case the animal was living under abnormal conditions, of which it must have been sensible, despite its partial freedom. The exhaled air had the same aromatic odor that is peculiar to the flesh, the excreta, the fat, and the steam from the boiling meat.

Thus the captive was studied for a number of hours, though but little else was brought out, for the radius of movement of which it availed itself was very small. Such observations as were made, however, were concerned almost entirely with the breathing. If one struck the animal with the tiller, it took each stroke with a slight shudder of the entire body. A more delicate sensitiveness of the skin could be made out at the corners of the mouth only. If one touched this region with the thumb, the dugong suddenly raised its head a hand's breadth from the bottom.

At evening the animal was rolled up onto the shore. During this process it thrashed about but little and allowed itself to be borne to land as quietly as a barrel. Not until it was choked did it repeat the tremendous strokes with the tail; at other times it moved neither the hinder part of the body nor the flippers. The latter were held against the breast, but if they were pulled away from the body, they remained in that position. For forty-eight hours it lay motionless. Its death was easy, for it was asphyxiated by quickly thrusting two gun wads into the nostrils during an inhalation. It raised its head, gave three mighty strokes with its tail and expired.

After this description, necessitated by the nature of the case, the biological details will again be systematically discussed. A little has already been said in regard to the manner of inspiration and expiration. Both processes take place out of water and exclusively through the nose. When the captured dugong was asphyxiated by closing its nostrils, it made no attempt to open and breathe through its mouth. These conditions in the dugong, it is interesting to observe, correspond exactly to those found

elsewhere in which the epiglottis is behind the velum or in front of it, and thus does not permit of a supplementary breathing through the mouth also (see Boenninghaus, :03, p. 84). Still, a similar topographical relation of the parts in question does not correspond to similar physiological phenomena, since in the Sirenia the velum palatinum and the epiglottis are very short (dugong, Owen, '38, p. 36; manatee, Waldeyer, '86, p. 245; Murie, '70, p. 178).

The dugong takes breath quickly, closes its nostrils, and sinks into the water. The closing results from the fact that the base of the nostril is raised as a slight eminence and pressed tightly against the top. It is interesting to observe that this procedure was also kept up while the animal was lying on the shore, and after each inspiration the nostrils were fast closed until the next breath was taken. According to Finsch, the closing of the nostril takes place through the action of a muscle which he does not indicate further. Ruppel ('34, p. 101) makes the incorrect statement that the nostrils can be hermetically closed by valves opening inwards and this fallacy is repeated by Brandt ('46–'69, p. 272). It is worthy of note that Turner ('94, pp. 319, 322, 326) found in the embryo and in the head of an adult dugong, valves ("valve-like flap," "plug-like valve"). No trace of such a valve can be demonstrated. The same structure, it has been claimed, has been found in the manatee. Brandt has previously asserted that in the Sirenia "aperturae nasales valvulis claudendae esse." Garrod ('77, p. 139) plainly speaks of a "flap valve" which forms the base of the nasal passage during the act of breathing but rises and completely closes the nostrils when it is shut. Likewise Brown ('78, p. 292), Chapman ('75, p. 461), Crane ('81, p. 457), and Noack ('87, p. 297) speak of a valve. Murie ('80, p. 32) had already rejected Garrod's statement and described the arrangement in the manatee as similar to that in the dugong, that is, that the base of the nostril is raised by contraction of a circular muscle and the opening is thus closed and that a free valve is out of the question.

In expiration there is a perceptible sound, that has been described above as a loud, long "blow." Klunzinger calls it a puff, Finsch a breath and a puff. Semon speaks of it as a singular hollow puff. Moreover, it is not accompanied by a discharge of vapor.

The increase in the length of the intervals between breaths, given above, is of interest. It is of course quite possible that the conditions of living and of breathing incident to the animal's long period of captivity were extremely abnormal, so that it is difficult to learn from them precisely the normal conditions. Nevertheless, we cannot be far wrong if we take as the average time between breaths a minute or a trifle less. The accounts of writers show great disparity on this point. Ruppel states that the dugongs come to the surface about once a minute. According to Klunzinger they do so every ten minutes and always about four times. Semon observed a large male that came up at intervals of from three to five minutes, and Finsch agrees as to these longer intervals. However that may be, it should be observed that the longest interval between breaths noted by us did not exceed two and a half minutes.

The dugongs, as above noted, feed chiefly by night and the same is also true of the manatee. To be sure, Noack ('87, p. 300) writes that they eat all day long without interruption, though Brown ('78, p. 295) had previously shown that as with nocturnal animals in general, they appear to feed at night only (see also Murie, '80, p. 24). The food and the feeding habits of the dugong have hitherto received very meager treatment. The animals lie, it appears, directly on the sea bottom, and with their thick lips graze leisurely upon the seaweeds (sea algæ, according to Ruppel) that grow on the rocks or the sea floor, or they tear them from the bottom. Klunzinger speaks of sea plants, phanerogams (Niades). According to Finsch and Semon it is chiefly sea grasses and species of Fucus, according to Fairholme, "grass-like seaweeds," that constitute the food supply. But it may be stated that the food of the dugong does not consist of the thick, dark brown seaweeds floating up free from the bottom, but rather of the two green phanerogamous plants which were present in the stomachs of all the dugongs killed, unmixed with any other vegetable remains. The dugong fishermen employed by Dexler paid no attention to the beds of thick, dark brown seaweeds that could be seen growing up from the depths, but kept a sharp and constant watch of the clear sand that was almost without vegetation. There only were traces of the dugongs to be found, and never in the rank forest of seaweeds.

At our request Professor Aschersohn of Berlin, had the kindness to examine the species of plants found in the stomachs of the dugongs, and determined the one to be *Halophila ovalis* (of the Hydrocharidaceæ) and the other a species of Zostera (*Zostera capricorni* Aschersohn). The latter grows as a dense or scattered low bed, while in Halophila the root stalk and petiole are hidden in the sand and only the small leaflets project slightly. These two plants do not occur on rocky bottoms. The Halophila growth is limited to a depth of about six meters below the low tide mark; higher up, the growth becomes sparser until it entirely disappears. The white sand, peculiarly flecked and spotted by the Halophila leaves, is the especial feeding place of the dugong. The slight depths at which the dugong's food plants can grow also explain why the animal spends part of its life in the shallow seas and part in the off-shore waters.

Among the beds of Halophila are the so called dugong's tracks which at once show us how the animal takes its food. The tracks are long, curved, or wavy furrows in the white sand, with sides parallel, about four fingers broad and from four to six cm. deep. They are completely denuded of the Halophila. Their age is determined by the condition of their edges; fresh tracks have raised, sharply defined edges rising from one to two cm. above the sea bottom. If the strong flood tide has swept over them once, the sand becomes washed away, the edges obliterated, and the depth less, until finally they are entirely washed away. These furrows, showing white through the dark water, indicate the presence of the dugong. They are produced by the dugong passing over the Halophila beds as it feeds, pulling up the plants with its palatal processes, seizing them and perhaps washing them free of sand and other extraneous matter after the manner of certain waterfowl (ducks), and then chewing them up with its molar teeth. The dugong trails are not made up of separate marks which would indicate that the food is not plucked or bitten off in tufts. Such plainly continuous trails could not be made by the animal's lying sluggishly at the sea bottom. Also the peculiar lateral mark made by the tusks[1] in case of the male is

[1] Finsch believes that the tusks serve for uprooting the sea grasses rather than as weapons, but the fact that they are lacking in the females, argues against this view.

explained by the method of feeding just described which necessitates their active share in this process. Finsch, however, speaks of dugong tracks that were found on bars left more or less dry at low tide and could be readily recognized by the cropped sea grass, the disturbed bottom, and the imprints that were left by the animals' bodies. The first of these marks is established by the description preceding, but we may very well doubt whether the last is possible. Nothing of the sort was certainly observed in Moreton Bay, Sandy Straits, Wide Bay, and the northern Coral Sea.

There can be no doubt that the sensitive upper lip plays an important part in the taking of food. We know from the numerous careful observations made on living manatees in aquaria (we may mention only Brown, Murie, and Noack) how extensively these animals use the upper lip in feeding. It is unnecessary to lay particular stress on the fact that the food plants of the manatee are considerably different from those of the dugong because of their different habitats. The feeding habits of the dugong, as described, likewise differ in a general way from those of the manatee.

The washing of the food plants in the mouth must be very thoroughly done. Moreover, the dugong in its progress stirs up a quantity of sand and other inorganic particles but for all that, matter of this sort is seldom found in its stomach contents.

It has been previously stated that the captured dugong while being pulled ashore, voided excreta and intestinal gases with the characteristic dugong odor. It likewise did the same while lying hauled out on the land. The fæces were rather solid, cylindrical, and greenish yellow to greenish black, aromatic but not fœtid; in the water they sank at once. Brandt ('69, p. 235) on the other hand, states that the intestinal contents of the Sirenia are strongly fœtid, that the excreta float on the water, and are similar in form to those of the cow or the horse. Chapman ('75, p. 460) records that the fæces of a captured manatee that appeared to be suffering from constipation, were very hard, and that a constant stream of gaseous bubbles was given out from the anus. Murie ('80, p. 22) in case of his manatee merely mentions the droppings. Noack ('87, p. 300) on the other hand, states positively that the

excreta of *Trichechus senegalensis* appear greenish brown and rather formless, and that they are usually seen in the water only. Brandt's description agrees with neither the dugong nor the manatee. The urine of the dugong is clear as water.

Unfortunately no exact observations could be gathered as to the temperature of the dugong. The captured specimen, when brought out on land grew remarkably cool. The rectum showed a temperature of 19° C. Immediately after its death the thermometer was thrust into a cut made towards the base of the heart. The dark red blood, laden with carbon dioxide, that gushed forth had a temperature of 17° C. One can therefore hardly express an opinion as to the normal temperature of the dugong, especially as the temperature of the air (taken by whirling the thermometer under a clouded sky) was from 12° to 18° C., and the animal had lain motionless for 48 hours. In addition the heavy body, weighing some 192 kilograms, pressed the easily fixed sternum hard against the heart, whereby the activity of the latter, the blood circulation, and consequently the body temperature must have been very much disturbed. The marked increase in the interval between breathings is also evidence for this. The beating of the heart could not be detected either by its palpitation or by auscultation. This dugong impressed one as an animal that had become cooled off, and whose temperature conditions (irrespective of its abnormal position on the shore, and the unusual pressure) were so sensibly disturbed that it had lived only a short time after being taken from the water. Moreover, observations on manatees taken and kept in captivity, show that almost always changes in temperature are the cause of the sickness and death of the animals (Chapman, '75, p. 461; Murie, '80, p. 23; Crane, '81, p. 460).

No voice or production of a sound on the part of the dugong could be detected beyond the blowing already mentioned, that accompanies exhalation and inhalation and it is similar to that of the dolphins. Finsch leaves the question open as to whether or not there is a real voice. The earlier writers speak of a hollow moan or snort in the case of adult animals, and of a short, sharp cry frequently repeated on the part of the young (Brandt, '69, p. 235). However, Brandt thought all these sounds were pro-

duced by dying animals only, for Steller likewise stated that the uninjured rhytinas never uttered a sound, while the wounded ones gave a sort of hollow moan. Also in the case of the manatee no trace of a voice has been observed (Murie, '80, p. 22) though Murie believes that this may be different under other circumstances. Nevertheless it is to be remembered that the Sirenia have no vocal cords and that therefore sounds or noises may perhaps arise through vibrations of the laryngeal cartilages and should thus presumably take their course out through the nose.

As regards the activitv of the sense organs the dugong as well as the manatee has reached a considerable degree of development. To many sense organs we are unable to assign a very definite function. This is true of the senses influenced by chemical stimulation, particularly the organ of taste, although as Gmelin ('92, p. 18) has shown, a taste organ is found in the manatee in the form of a so called papilla foliata. The care shown in the selection of food likewise points to a certain taste function. It is still more difficult to demonstrate the function of the organ of smell since the olfactory region is a nasal tract that is hermetically closed when under water. And yet Chapman claims that in conformity with the well developed bulbi olfactorii, the sense of smell must be very keen, for it was observed that his captive manatee seemed to become aware of food thrown in the water through its sense of smell rather than by any other sense. Brown ('78, p. 295) says the same, referring to Chapman.

Boenninghaus (:03, p. 91) has pointed out that mammals that seek their food in the water, can make no use of their sense of smell in obtaining it because the nose is tightly closed in diving. Even if this were not the case, he continues, mammals would still be unable to smell under water since the necessary stimulus for their olfactory nerves consists of scent particles which are held in suspension in the air and not, as with fishes, those that are suspended in the water. The disuse of these organs in the case of whales has led to their partial atrophy or total disappearance. Thus in the toothed whales the olfactory nerve is lacking, and correlated with this is the reduction of the exethmoid bones. In the Sirenia, however, in spite of a reduction in this bone, an olfactory nerve and bulbus are well developed, and this, too, not-

withstanding the objections just mentioned to the possibility of a smelling function. This possibility becomes a probability if not a reality by the observations on the manatee given above. From these observations it follows that in the Sirenia, at least, there is no connection between the reduction of the exethmoids and that of the olfactory nerve as there may be in case of the whales. It is also clear that the olfactory nerve as a functional structure must be capable of perceiving chemical stimuli that utilize water as the carrying medium instead of air as with land mammals. This assumption, of course, implies not only a partial functional adaptation of the olfactory nerve but it also limits such an adaptation to the herbivorous Sirenia alone. Finally we must also assume that the chemical stimulus, since it cannot reach the olfactory membrane in the usual way, must take another course, perhaps by way of the mouth, pharynx, and choanes.

One more observation on the reflex irritability of the nasal membrane may be added here. Before the death of the captive dugong, Dexler endeavored to squirt water into the animal's nose as it drew in a breath. Instantly there came so violent an expulsion of the fluid — which had barely entered the nostril — that it was blown into a fine spray. The reflex was astonishingly violent and quick, and after it had taken place the nostril openings were fast closed as before. Thus the breathing movement that had been begun, was not completed. Surely so prompt a reaction is of the greatest importance for aquatic mammals. The action by which the nose is closed in case of the dugong is thus two-fold: voluntary and reflex. Water pressure as an aid is not necessary, or at least only auxiliary.

The dugong's sight must be characterized as rather poor. Otherwise it would be impossible to capture the animal with so roughly constructed a net, as is actually done. Nets from 80 to 150 meters long and from 5 to 6 meters deep are so disposed over the dugong's feeding grounds as to form a vertical wall. If a dugong comes in contact with the net, then it is usually all up with him; but a dolphin or a shark is never captured in so simple a manner. To be sure, the dugongs avoid the nets more easily on clear nights and for this reason the best time to take them is during the nights of the new moon. The cords of the

net are colored brown also. But if one is lucky he may capture the animals during the full moon as well, and even with new nets of shining whiteness. A further proof of the poorly developed vision is the fact that the captive dugong did not notice very much the waving of a white or a black flag and that not infrequently no notice was taken by the dugongs of the noiseless approach of the boat so that it was possible to observe these animals at very close quarters. Semon has remarked the same thing and the fishermen employed by Dexler asserted that they had repeatedly sailed right over feeding dugongs. This might be due, however, to the fact that it does not seem particularly shy (Semon) or that it is but little concerned for its own safety (Finsch). Feebleness of vision has likewise been recorded in case of the manatee (Chapman, '75, p. 454; Brown, '78, p. 295).

Investigation of the eye in case of our captive dugong was very difficult and therefore inadequate. For in order to do this one must lie directly beside the animal on the sand, and as may be readily seen, this is, to say the least, disconcerting when one does not know what movement the creature may make next. Moreover, the focal illumination was considerably hindered because the bulbi were deep set and constantly held pointing slantwise forward and downward, and the slit between the eye lids was narrow. Furthermore there flowed from the conjunctival sac such a quantity of tough, stringy secretion that the eye opening was constantly obstructed as with a thick plug.

This had first to be removed and the short intervals before its re-formation were utilized in a rapid study of the front portion of the eye. It was impracticable to expose the bulbus by opening the eye lids with one's fingers for these were closed tightly at the slightest touch. If they were forcibly pressed apart the nictitating membrane was then pushed up and the bulbus retracted in such a way that it disappeared under the membrane and the periorbital masses of fat that were forced forward. After five or ten minutes there appeared at the bottom of the fatty funnel thus formed a bit of the cornea like a small black spot which became no clearer in spite of long waiting. When the finger was removed the eye returned to its proper place, but for hours after it remained more deeply in the socket than it had

been before the investigation. This retraction movement took place independently of the position of the other bulbus.

By combining a number of partial observations, only the following particulars could be made out: a very strongly curved cornea, a considerable mobility of the blackish brown iris which reacted promptly to light, an indistinct radial striation, and a circular pupil.

The use of the ophthalmoscope seemed at first to be attended with no results, for nothing but a deep black was visible. Then at a chance motion of the dugong's eye the small, round rose-colored papilla or the disc of the optic nerve came in sight. Thereupon further exploration of the retina was made though without additional results. The entire area of all four quadrants consisted of a deep black continuous tapetum nigrum in which no details could be made out, as is likewise true to some extent in case of the ventral portion of the fundus of the horse. In order to perceive clearly the few extremely delicate capillaries that radiated to the tapetum from the upper rim of the disc required an increase of the observer's myopia from $2\frac{1}{2}$ to 5 dioptria from which may be deduced the degree of short-sightedness of the animal when out of water. The refraction of both eyes was the same.

It is noteworthy that the dugong also exhibited a certain dislike for bright light. At least one may so conclude from the eagerness with which it sought the shadow cast by the hull of the cutter.

In the manatee the pupil is round in life, but is transversely oval when the animal is dead (Murie, '80, p. 24). The dugong's pupil did not change shape after death. As in the manatee the nictitating membrane is well developed and freely movable. The eyelids are contractile and can be brought together until there is only a small slit, 12 mm. long, that remains not quite closed. The complete isolation of the bulbus from the exterior is effected by the nictitating membrane and the periorbital fat. The lids when closed are deeply wrinkled in a radial fashion, on account of the very strong orbicular contraction. This fact disposes of Pütter's (:03, p. 369) assumption based on the study of an embryo dugong whose eye slits were 5 mm. long and 3 mm. broad,

that the eye lids as in case of the whales cannot be opened nor approximated. The copious secretion of the conjunctival sac has already been mentioned. In our captive the string of slime was of the consistency of the white of an egg, was as thick as one's finger, and flowed over the entire eye and down to the ground. That this secretion might be due to the irritation caused by the atmospheric air or the unaccustomed light immediately suggested itself, but in all the animals taken the secretion was similar without any difference in regard to mass, thickness, consistency, nor transparency and thus possessed properties not present in a catarrhal flow. The corneal reflex was easy to demonstrate and the eye lids were always held open.

The eyes of the dugongs that were dead when taken, were always injured even if they had hung in the nets only six or eight hours. In such cases there were uneven scratches with finely serrated edges, spreading superficially or even onto the membrana descemeti. They were always interior to the poles of the cornea, which lay free in death. The lens usually showed star-shaped to diffuse whitish cloudy spots that generally became more pronounced the longer the body was allowed to remain in the water. These spots were doubtless phenomena incident to death. The secretion of so great a quantity of slimy viscous matter from the conjunctiva is a protective adaptation to keep the surface of the eye from injuries from the sea water or its plankton fauna. If the slimy covering fails then the bulb of the eye is without protection. In this way are caused the scratches above mentioned, of whose traumatic nature there can be no doubt. In some specimens this even results in the eye lids becoming so abraded that they bleed freely.

The presence of a slimy protective coat for the eye has also been demonstrated for the whales, only in them it is not watery and mucous as in the dugong, but oily for otherwise it would be too easily washed away by the sea water (Pütter, :03, p. 370). Thus in the Cetacea a change of function has taken place in the glands of the eye as an adaptation to the conditions of aquatic life, and their products are likewise changed.

The copious secretion of mucus from the dugong's eye has long been known to many of the islanders of the Malay archi-

pelago. All sorts of fantastic tales are associated with the so called dugongs' tears, in regard to their use as a powerful charm. Brandt ('69, p. 274) speaks only of the young dugong's shedding tears and that these were carefully gathered because they aroused in the possessor an affection as strong as that of the female dugong for its young. This belief was taken advantage of by the German and French perfume makers in order to assure a better market in Java for their perfume imported under the name of "dugongs' tears," "ajer mata doejoeng" (Dexler, :05, p. 200).

In contrast to the senses hitherto mentioned, that of hearing appears to be very well developed in the dugong. Both in the water and on the land the animal seemed to be much more affected by sound impressions than by those of sight. The dugong lying on the beach winced considerably at a sharp squeaking sound made by drawing in air between the puckered lips, as do also the guinea pig and the mouse. Only after numerous and quickly repeated stimuli of this sort did it remain motionless. Whether its ear was acoustically over sensitive with the absence of water pressure could not be determined. Nevertheless some sort of a stimulating influence is within the range of possibility since the meatus acusticus externus de norma transmits the pressure of the water to the ear drum. Also in the great size of the ear bones is seen an adaptation for hearing under water and not in the air, just as in whales (Boenninghaus, :04, p. 282). Evidence for keenness of hearing in the dugong is also found in Finsch's statement to the effect that in setting out the hunting-scaffolds for capturing the dugong, one must work with great care since the slightest rattling of these is said to be enough to frighten the animals away. Also in harpooning them one must proceed with absolute silence (Fairholme). Dexler's fishermen gave the floats of their nets a wedge-shaped form in order, as they claimed, to obviate the slight noise produced by the waves in striking floats of any other shape, and so frightening the animals away. But as a matter of fact the dugongs were rather frequently captured when the floats splashed loudly.

Besides the sense of hearing, we must also accord a fairly good development to that of cutaneous sensibility. The large upper lip appears to be very richly provided with nerves of feeling and

as is evident from its anatomical construction, it is especially adapted for a manifold touch function, a fact that is of the greatest importance in the procuring of food. Apparently it serves in some degree to offset the seemingly poor eyesight, so that the animal in its wanderings over the beds of seaweed may be acquainted of the presence of blocks of coral, stones, and the like. The finely developed sense of touch in this organ is also shown by the fact that it was never found to be injured, in contrast to the skin of the rest of the body.

The presence of numerous scars and scratches on the skin of the back and sides of the body is characteristic of the dugong. As to their origin one can only guess. A very small portion of them may be set down as due to the wounds from the tusks of the males. Even in the oldest of 25 specimens examined, these tusks projected only 32 mm., and on their median sides they were almost entirely covered by the palatal processes. They are therefore very poorly adapted for making wounds. Possibly the animals wounded themselves in their endeavors to scrape off clinging parasites. The fishermen give a different explanation: they maintain that they have often seen the dugongs while at play, wound their backs on stones and corals as they rolled or swam about on the bottom. They thought the dugongs did this particularly over beds of Pinna shells, but it was impossible to determine this point.

There is little to be said in favor of the much discussed intelligence of the dugong. We have thus far seen no convincing evidence for according a particularly high degree of acuteness to a single one of the animal's senses. The senses of hearing and touch may be deemed the most highly developed; then, in a descending series, sight, taste, and smell. But even the keenness of hearing accorded the dugong cannot be compared with that of a really very keen-eared animal; otherwise the fact would be inexplicable that it is possible, though rarely to be sure, at times to sail up to feeding dugongs. When Dexler saw the herd of dugongs, previously mentioned at Moreton Bay, his men were rowing with splashing oars and without particular precaution. It must also be recalled that the often emphasized sound stimulus in water may frequently be communicated by the sensitive skin

and mucous membranes of the head as well. The other senses, as before mentioned, are much less well developed. Considering the manifestly slight capabilities of the peripheral sense organs, it can hardly be concluded that the central nervous system has reached a high state of development. In fact, the brain of the dugong is not only relatively small — $\frac{1}{400}$ to $\frac{1}{600}$ of the weight of the body — but as we shall show in a later paper, it is so lowly organized that only a comparatively slight degree of intelligence may be presumed in this animal. A further proof of the stupidity of the Sirenia is found particularly in their behavior towards enemies, in their defencelessness, and in the ease with which they may be killed and exterminated.

Another question which we will here treat at further length is that of the use of the flippers. While on the one hand it is assumed (Freund, :04, p. 346, and elsewhere) that the flippers of the Sirenia are used as paddles and balancing organs, on the other hand it is supposed (Abel, :04, p. 186, etc.) by way of explaining certain anatomical changes, that their function is that of supports. In the dugong, particularly in case of the specimen that lay on the shore, one could clearly see that movement from place to place in the water was accomplished solely by means of the caudal fin. The pectoral limbs were held motionless at the sides, and directed backwards. If one endeavored to roll the dugong over on its side, it began to strike out with its tail but allowed its pectoral limbs to remain where they were. Active movements of the flippers for the purpose of locomotion on dry land were not observed.

There has been very little recorded as to the movements of the dugong on dry land in general, where a use of the appendages in locomotion is to be presumed. Klunzinger makes only the indirect statement that in the northern part of the Red Sea they are frequent in winter especially in December and January, and that otherwise they seldom go to the land. Finsch (:01, p. 10) speaks of an account by Leguat who was led to Rodriquez, in 1691, mainly on account of a dugong that was seen lying on the shore. Still, in Finsch's opinion this was a stranded animal since the dugong does not voluntarily go onto the land, and moreover has nothing to seek there. If a dugong be captured and

thus forcibly brought to land, it may live 24 hours he was told by old Kabury on Palau. This observation is corroborated by that on our dugong which passed an even longer time — 48 hours — on land. It appears therefore that the dugong has not been actually observed to come out onto the land of its own accord, and in our opinion such a procedure is out of the question since the pectoral limbs are insufficient to enable the animal to do this. In no wise can it be established, as Brehm would have it, that "one can at least assume that those dugongs that have been seen lying on the shore were left by the ebb tide and were too sluggish to push their heavy bodies into the water again, preferring rather to wait quietly the next flood tide." They are simply incapable of using their anterior limbs, even as supports, on dry land. The possibility still remains that they support themselves on their flippers while gathering their food in the water. But against this supposition, in the first place, are their observed manner of feeding and the so called dugongs' tracks. In the second place, the difference in specific gravity between the animal's body and the supporting medium, cannot, in view of the considerable mobility of the dugong, be such as to entail any great burden on the limbs. Thirdly, the slender form of the appendages, their relatively small size, and finally the uninjured epidermis on the parts in question, furnish evidence against their use as supports in the water. Also in the case of the manatee, here adduced for comparison, the use of the flippers as organs of support is denied rather than maintained. Moreover, Brandt cites three authors who conclude from the manner of capturing the American manatee, that it is incapable of getting back to the water (by the aid of the limbs) if left up on the dry land. Garrod ('77, p. 139) says very decidedly that his manatee seemed *wholly unable to move either forward or backward on the land*. It made use of the limbs in sidewise movements only, at the same time twisting the body and tail. Chapman ('75, p. 461) and Murie ('80, p. 26) observed that their manatees swam quietly about at the bottom of the aquarium with the body sharply bent and the head and tail pointed downwards. Neither author says a word about their supporting themselves on their flippers, and Murie figures the animal in the posture described, with the limbs hanging down. He men-

tions their aid only in the taking of food. Brown ('78, p. 296) brings up still another argument against the possibility of a manatee being able to leave the water by aid of its flippers, namely the weakness of these organs, and his investigations into this matter also resulted negatively. Crane ('81, p. 457) makes a similar statement, basing his opinion on the generally clumsy movements of the animal when on dry land as well as on certain other considerations. Opposed to these observations are only the statements of Cunningham ('70) and Noack ('87, p. 299). The former saw a manatee support itself above the water by its flippers in order to crop the grass at the edge of the shore. This was done in such a way that one limb rested upon the shore. The latter author goes still further, for he states that the manatee is able to come out and move about on the land. "The animal (*M. senegalensis*) can actually move from place to place, though in a hobbling and unsteady manner. In so doing it supports itself on its wrists [!] and the outer edge of the forwardly directed hands, moving them alternately, and thus it progresses forward, though slowly, wriggling its body as it goes." But one may also suppose that the wrigglings of the body were the primary and locomotor movements, while the motions of the flippers might have prevented the body from falling over. In any case the position of these limbs as described is very remarkable! Noack relates that his manatee while in the water used its flippers to remove from its mouth pieces of bread that had proved too large. But as for a supporting function of these organs while in the water, Noack likewise knew of no evidence.

To sum up, it must be said, then, that scientific observation on the sea cows (for in case of the rhytina, also, Steller mentions that they are unable to move about on land) has hitherto produced but slight evidence that would permit us to assume so considerable a use of the flippers for body-supports as would explain the development of many anatomical details. Nevertheless, theoretically one may suppose it has only chanced that the use of the limbs as supports has been so seldom seen. But on theoretical grounds also, considerable objection may be raised against the evidence brought forward by Abel (:04, p. 166) as has already been done in the course of this discussion. We should remember

that the Sirenia have arisen from air-breathing land forms of Mammalia; further we should not forget that their terrestrial type, with its adaptations of the body to pressure and weight, is greatly modified by adaptations to an aquatic life. Thus as we trace the evolution of the Sirenia, their mechanical adaptations to terrestrial life will be less and less noticed while those for aquatic existence will increasingly force themselves upon our attention. In like manner the anatomical changes brought about by these adaptations show the same progression. Such convergent anatomical changes in animals of the same biological environment are due to the influence of identical causes. In the case of these water mammals where proof of such changes is impossible to-day, we need not always assume different causes; here the same causes were acting on different objects (*e. g.*, Cetacea and Sirenia) and therefore it is conceivable that the same causes may bring about different results.

The dugong is the host of great numbers of parasites, both external and internal. On its back, as with whales, numerous barnacles establish themselves; a few Balanus but mostly Chelonobia. Internally, at the opening of the inner nares, on the dorsal surface of the velum palatinum, but particularly in the Eustachian tubes of both sides, were found numerous leaf-shaped trematodes from 3 to 5 mm. long clinging to the membrane in a mass of an hour-glass shape. These must have been identical with the *Opisthotrema cochleare* described in 1884 by Fischer. He had received them from Semper (of Würzburg) who collected them in the Philippines from the tympanic cavity of the dugong. Leuckart also, in 1875, described a trematode from the Eustachian tube of the dugong under the name of *Monostomum dujonis*. Von Linstow ('78) considers both forms as probably identical. The favorite habitats of these trematodes give, we believe, an indication of the path by which the infection has spread in case of the dugong, namely, from the nose, to pharynx, Eustachian tubes, and tympanic cavity. To be sure, Boenninghaus (:04, p. 259) has controverted the idea that in case of the parasites of the whale's ear the path of infection has been through the pharynx and the Eustachian tubes. He himself mentions a nematode, *Pseudalius minor* Kuhn, from the ear cavity of Phocæna. Moreover, von

Linstow records *Strongylus arcticus* Cobb from the ear of the beluga, and *Pseudalius alatus* from the Eustachian tube and the pharynx.

In the alimentary tract of the dugong, trematodes occur in the gut and the cæcum. In the small intestine some very large worm masses were observed, whose composition could not be fully determined. In addition, a species of Ascaris has long been known from the digestive tract and numerous specimens of this were also found in the glands of the stomach. It is *Ascaris halicoris* Owen, also wrongly called *Ascaris dugonis* Brandt. Whether the Ascarid seen by Steller in the rhytina is identical with that found in the dugong cannot now be determined. Two endoparasites are also described from the manatee: a nematode, *Heterocheilus tunicatus* Diesing, and a trematode, *Amphistomum fabaceum* Diesing (von Linstow, '78, '89). Chapman ('75, p. 456) found the large intestine of his American manatee filled with the latter.

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CORRESPONDENCE

Congress of Oceanographers

Editor of the American Naturalist.

Sir:— I enclose copies of correspondence in regard to a Congress on Oceanography which is to be held in connection with the Colonial Exposition at Marseilles, France, in 1906, and in compliance with the French Ambassador's request, invite your attention to the desire of the organizers to secure the coöperation at the Congress of the associations and individuals named in the accompanying list, the *American Naturalist* being among them.

I am, sir,

Your obedient servant,

ROBERT BACON
Acting Secretary

DEPARTMENT OF STATE, WASHINGTON
October 11, 1905

Translation of Letters from French Embassy

Mr. Secretary of State.

The Minister for Foreign Affairs has sent me a letter in which Mr. Charles Rouse, Commissioner General of the Colonial Exposition to be held at Marseilles in 1906, expresses the wish to have the attention of the Government of the United States invited to the section of Oceanography of that Exposition.

In order to comply with this request, which is particularly commended by the Minister of Commerce and Industries, the French Ambassador desires to request the Federal Government kindly to invite those persons in America, who make a study of oceanography, to take the result of their studies to the Marseilles Exposition, communicating to the particular ninth section of said Exposition, the results of their research and to participate in the Congress on Oceanography which will be organized under the auspices of the section in question.

I shall thank Your Excellency for kindly informing me in order

that I may notify my Government, of the replies which the Department of State shall receive to this communication.

Accept, Mr. Secretary of State. assurances of highest esteem.

Des Portes

Embassy of the French Republic
in the United States, Washington
October 2, 1905

Mr. Secretary of State.

Under date of September 11 last, this Embassy had the honor to invite attention of the Department of State to the interest felt by the Republic in the Colonial Exposition at Marseilles, and particularly the Section of Oceanography and Sea-fishing, which is a part thereof. Referring to that communication as well as to the kind reply made by the Department of State, I take the liberty of transmitting herewith to Your Excellency a list of the associations and individuals who, in the opinion of organizers of the projected reunion, would be especially apt to contribute to its success.

I should be very grateful to Your Excellency if you would request them to signify their adhesion to this important international manifestation which promises to be of great scientific as well as practical interest.

Accept, Mr. Secretary of State, assurances of my high esteem.

Jusserand

Embassy of the French Republic
in the United States
Newport
September 11, 1905

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THE AMERICAN NATURALIST

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DEVOTED TO THE NATURAL SCIENCES
IN THEIR WIDEST SENSE

CONTENTS

			Page
I.	The Unity of the Gnathostome Type	DR. H. AYERS	75
II.	Old Age in Brachiopoda—a Preliminary Study	DR. H. W. SHIMER	95
III.	The Habits of *Necturus maculosus*	PROFESSOR A. C. EYCLESHYMER	123
IV.	**Notes and Literature**: ***Zoölogy***, Kellogg's American Insects, Kingsley's Elements of Comparative Zoölogy, Punnett's Mendelism, Hantzsch's Birds of Iceland, Holder's Half Hours with the Lower Animals; Notes, *Additional Records for New England Crustacea* (J. A. Cushman); ***Botany***, Smith's Bacteria in Relation to Plant Diseases, Farlow's Index of North American Fungi, Osterhout's Experiments with Plants, Sargent's Manual, Notes, The Journals; ***Geology***, Notes		137 143 155

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THE UNITY OF THE GNATHOSTOME TYPE

HOWARD AYERS

SINCE zoölogists have recognized the simple nature of the Cyclostome fishes there have been many contributions to our knowledge of their structure and many discussions as to their nature and their true zoölogical position.

The increase in our knowledge of the anatomy of amphioxus and the clearing up of its development by the investigations of Kowalevsky, Hatschek, and Willey, have increased the amount of interest in these discussions and have added to the subject an entirely new phase in that the amphioxus, instead of being longer considered a zoölogical curiosity, a degenerated or aberrant form, has become the center of an intense and searching discussion of the origin and relationships of the Vertebrata; and amphioxus has thus come into its own by being recognized as an ancestral form in the genealogy of the vertebrate stock and the oldest living relative and representative of this group of animals.

We can now see clearly enough that the Marsipobranchia and the Acrania both stand in the relation of ancestors to the vertebrates above them, and there is no longer any doubt, while recognizing to the full the many unsolved problems in connection with its structure and development, that amphioxus belongs to the group of forms, the Prospondylia, predecessors of the Archicrania, from which the Cyclostomes are directly descended. It must

be admitted that the gap between amphioxus and Bdellostoma is very great, both as regards time and the amount of the transformation of structure which it has undergone, and that in many things we cannot yet satisfactorily explain the manner in which this transformation has come about.

On the other hand, we may with certainty say nearly as much about the gap between the Cyclostomes and the other Gnathostomes, but the absence of complete knowledge has never been permitted to blind unprejudiced minds to the just estimate of the known facts in any zoölogical problem.

Recent advances in our knowledge of the Marsipobranchs render Haeckel's estimate of the amount of difference between the Cyclostomes and vertebrates above them quite untenable.

He says (*Syst. Phylog.*, vol. 3): "Eine tiefe morphologische Kluft und ein entsprechend langer historischer Zwischenraum trennt beide Classen der Agnathonen nicht bloss von den echten Fischen, sondern auch von allen übrigen Vertebraten die wir in der Hauptgruppe der Amphirhinen oder Gnathostomen zusammenfassen."

There is no reason why we should, at the present time, follow partisans of any genealogical theory of the origin of the vertebrates in ignoring the many anatomical and embryological facts which we now possess and which clearly enough establish the genetic relations of these forms.

Some writers are too prone to assume the existence of large groups of extinct forms intermediate between the groups of existing vertebrates and between these and those forms from which the vertebrates have descended — which have disappeared without leaving any trace of their structure in recent forms.

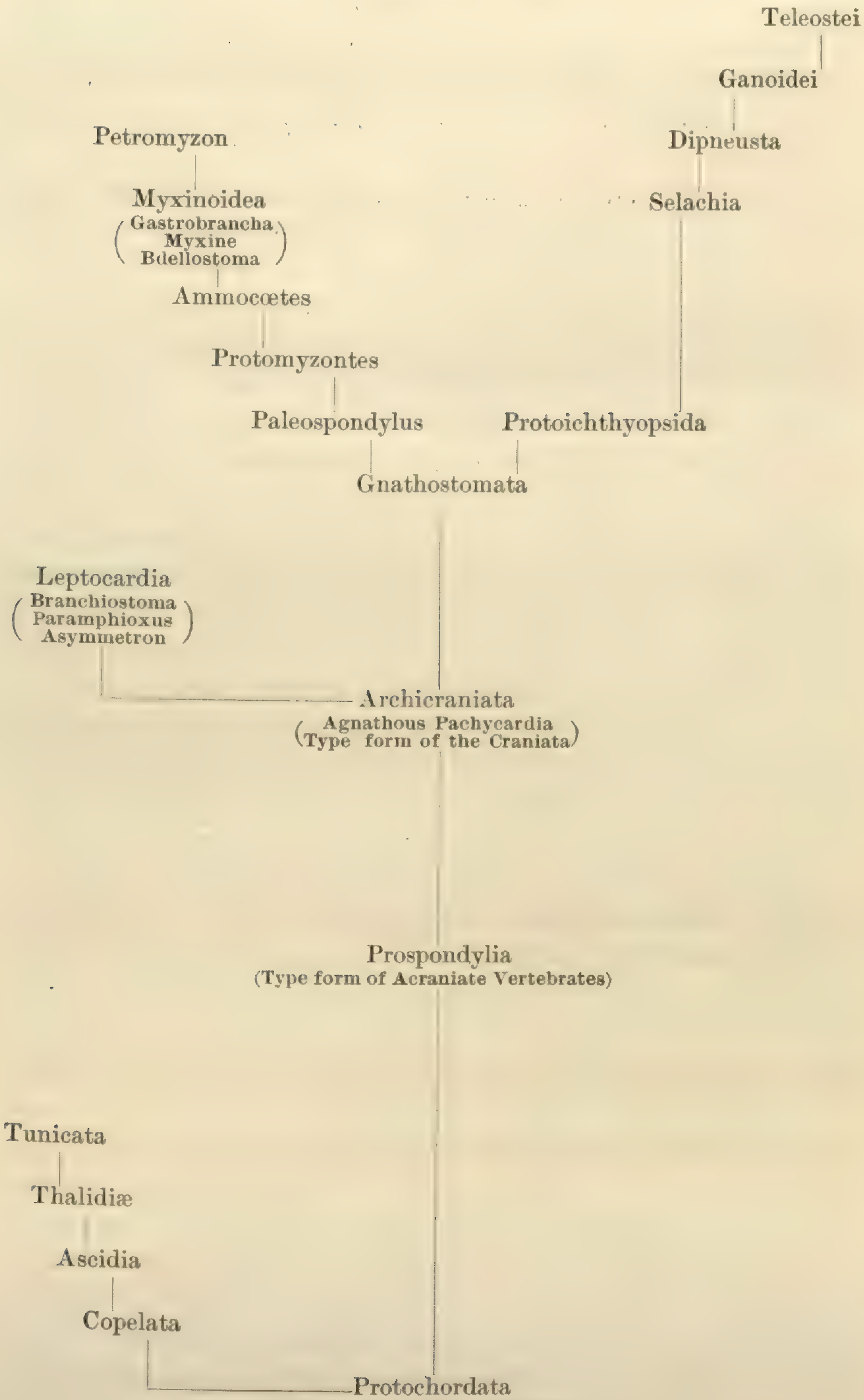
There is neither anatomical nor embryological ground for the removal of amphioxus from the vertebrate class, and we may express our view of the relation of existing forms thus:—

VERTEBRATA

Amphioxus — Leptocardia — Acrania
All others — Pachycardia — Craniata

and by the following table:—

Genealogical Tree of the Ichthyopsida



Before taking up the question of the unity of the Gnathostome type, a brief consideration of some of the general features of the vertebrates will clear the way for a better understanding of the arguments and facts which bear on the solution of the problem.

First of all we may well consider amphioxus as a typical ancestral vertebrate.

The Vertebrata, as we find them to-day, form a morphological unit in much the same way that the birds form a closed group — and it is only through paleontology that the shading off of the group into lower forms is to be found or proven. That the vertebrates have arisen from a common source is a statement which cannot to-day be questioned, for the present state of our knowledge of their anatomy, ontogeny, and physiology is a practical demonstration of the problem. Each increase in our knowledge only makes the demonstration stronger. All three fields of investigation — comparative anatomy, comparative embryology, and paleontology — unite in one affirmation of this fact. All three show that there has been an orderly progression (to use only living forms as examples) from amphioxus to man. No one can read Hasse's *Das natürliche System der Elasmobranchier*, to mention only one of many similar investigations, without having the fact of the historical succession of these early vertebrates indelibly impressed upon his mind. The genetic relationships of this procession of Selachians from the earliest geologic ages, when the fossiliferous records of the vertebrate stock were begun, is proven by the comparative morphologic study of the skeletons of extinct and recent forms and this proof is strengthened by the as yet only partial, embryonic record which has been worked out by many investigators. The course of development is marked by the retention in all living forms of all the divergent branches of vertebrates, from amphioxus up to the mammals, of the same fundamental arrangement of organs and systems of organs, and by the same general cellular structure. The variations in arrangements of the organs and the differences in the histological details of the tissues are not greater than the variations of the external form or of the shape of the internal organs. These are large facts of fundamental value, and have a greater morphologic worth than the many minor variations can possibly have, even when

taken together. They prove the essential unity and genetic relationship of all the Vertebrata.

Semper's view that amphioxus is not a true vertebrate has long since been effectively disproved, and the most forceful part of the proof that amphioxus does belong to the ancestral stock of vertebrates is contained in its simple palingenetic development, at least so far as the earlier stages are concerned.

The method of laying down the gills up to the time that the secondary gills are established, is in every way comparable with the processes of gill formation in Bdellostoma. The transformation of the brain up to the apex of its development is similar to the development of the vertebrate brain, the only difference being that it stops its growth in a very primitive stage of the Craniate brain. The differentiation of the tissues is in every respect the same as that occurring in other vertebrates, except that the process of tissue formation does not go as far, while some tissue systems, which appear in upper vertebrates, are never developed in amphioxus. For example, the masses of connective tissues common to other vertebrates, in the form of true cartilage and bone, are not even hinted at. The statement that its tissues are epithelial is most erroneous.

The lack of formation of such structures as jaws, chambered heart, lacunar hepatic gland, cartilaginous skull, etc., is certainly to be put down as a palingenetic characteristic.

When we seek the type form of the vertebrate stock we are forced to look to the invertebrates as the source of origin. Almost all the groups of the Metazoa have been searched for the ancestral type, and in nearly every case a type-form has been discovered which shows the means of descent sufficiently satisfactory to the individual zoölogist to warrant a long and careful discussion of the manner in which the morphologic and physiologic changes have come about that have resulted in producing the vertebrates as we find them to-day.

Three types of structure have, however, been used more frequently than the others. They are, respectively, nemertean, annelid, and arthropod. All three of these types possess a sufficient number of characteristics in common with the vertebrate type to warrant many parallels being drawn between each of them and the vertebrates.

The great difficulty in the way of accepting any of the well developed jointed invertebrates as the ancestral vertebrate type lies in the necessity of a revolution of the body through an angle of 180 degrees, whereby the dorsal surface of the invertebrate becomes the ventral surface of the vertebrate; and also in the concomitant necessity of the formation of a new mouth and the total disappearance of any trace of the old mouth. While there is, at the present time, abundant evidence to show that the functional mouth of the vertebrate of to-day is a neomorph, and that the original mouth was situated at a point anterior and dorsal to the present location, it does not follow and the evidence does not tend to show, that the old mouth corresponds in any way to the mouth, *e. g.*, of the arthropod.

This translocation of the mouth from the invertebrate ventral to the vertebrate ventral surface must have been connected with the reduction of the circumœsophageal nerve ring, and with the total disappearance of that section of the stomodæum which connects the mesenteron with the mouth by preforating the nervous system through the territory of the circumœsophageal nerve ring.

The fact that the stomodæum no longer perforates the nerve ring is a fact which must be satisfactorily explained by in some way discovering the stages through which the transformation has passed from the invertebrate to the vertebrate condition, or the genealogy of the vertebrate stock with the arthropod as the ancestral form cannot be satisfactorily explained.

There is great doubt that the vertebrates are derived from a highly organized annulate invertebrate. They are more probably a distinct branch split off from the unsegmented worms, and developed independently. Many are the theories which have been offered to harmonize the annulate and the arthropod conditions with the vertebrate, but none of them have accounted for a sufficient number of facts to warrant their general acceptance, and, as above stated, the main difficulty has consisted in the inability to picture the revolution of the invertebrate body in such a way as to make it physiologically possible in living forms.

It matters not what position we take with reference to the origin of the vertebrate stock, when we arrive at the stage of development represented by amphioxus we are compelled to admit, in the light

of our recent knowledge, that amphioxus is a true vertebrate, lacking it may be the first trace of the craniate skeleton, and lacking many of the other features which are characteristic of most of the existing vertebrates, but is nevertheless, the only existing form which serves as a connecting link between the simple ancestral type of structure and the more complex anatomical and physiological conditions of the higher vertebrate.

Some zoölogists have recently re-uttered Semper's opinion, that amphioxus is not a true vertebrate, but such restatement of Semper's opinion is justly to be compared to the restatement of the opinions of the older zoölogists, who at various times held amphioxus to be a worm, a mollusc, and a tunicate. Instead of making assertions as to what amphioxus is or is not, the only scientific method of solving the problem of its actual position in the animal series is by a careful study of its structure and a comparison of this with the structure of the lower vertebrates. Such comparison proves beyond the shadow of a doubt the relation of the amphioxus to the lowest fishes.

A review of some of the salient features of amphioxus' anatomy will not be out of place at this point. As regards the form of the body, all zoölogists recognize the fact that the shape of the vertebrate body is a result of the direct response of the organism to its environment, particularly the necessity of locomotion. The lancet shape of amphioxus is due to its burrowing habit. The lack of paired appendages is due to the fact that amphioxus represents the stage of the development of vertebrate structure when such appendages had not yet been developed. The median fin folds are well developed, both in the head and in the caudal region, and serve the same function in essentially the same way that they do in other vertebrates. There is no trace of a *quasi* lateral fin fold, nor of the buds of lateral appendages in the amphioxus, but neither of these are found in the Cyclostome fishes, which are much more highly organized than amphioxus.

The lack of the development of paired appendages in amphioxus and the Cyclostomes is not a mark of degradation, or degeneration, as some zoölogists would put it, because the whole course of their development and the facts of their morphology prove conclusively that these structures were not called forth by the response

of these animals to the stimuli of their environment in the direction of pedal locomotion on the sea bottom. It is highly probable that these appendages arose as ventrally projecting bar-like structures, to enable the bottom-living forms (since all were bottom dwellers to begin with) to move more readily from place to place on the surface of the sea floor while remaining in contact with the sea floor, thus avoiding the necessity of the more difficult feat of balancing themselves in the lighter ambient fluid above the earth floor, in the effort to effect a change of place.

Paired appendages then *did not arise as fins* for the purpose of *balancing the animal in the water*, but the paired fins of fishes have been developed by the transformation of the primitive paired organs of locomotion, of which the paired appendages of the Amphibia and their descendants are the direct and, in their simplest forms, the least modified derivatives.

When one studies the life habits of amphioxus and Bdellostoma in their natural element and, at the same time, the history of their development, he no longer entertains the idea that these animals have lost paired appendages once possessed by their ancestors, but will, and can only, say that they are the ancestral forms of animals possessing paired appendages, and that in the case of amphioxus and of Bdellostoma we have two stages in the response of the vertebrate stock to the stimulation of the environment looking toward the formation of locomotor appendages.

They are both bottom dwellers of necessity, although they take occasional excursions into the superambient water, but quickly fall back, from the force of gravity, to the bottom. These excursions into the superambient liquid are effected by the motion of the caudal fin from side to side. This fin is the main organ of locomotion used by all fish-like vertebrates for progression through the water.

When amphioxus strikes the bottom after such an excursion, it lies quietly upon its side, since it is unable to coil its body sufficiently to lie on its ventral edge. Most of its life it passes buried in the sand. To enter the sandy bottom in which it lives, it first makes an excursion into the superambient water and then descends head first upon the sandy bottom, boring its way among the particles of sand. When swimming it maintains its body in the dorso-ventral position.

In the case of the Bdellostoma we have a very different condition. The Bdellostoma possesses a body remarkable for its flexibility and its elasticity, and is fitted not only to swim in a dorso-ventral position, but during life, when it rests upon the bottom, always does so with a dorso-ventral orientation. While amphioxus shows a distinct inability to orient itself and maintain equilibrium in this position for any but the shortest periods of time, Bdellostoma exhibits in a high degree the capacity to maintain its position with ease, accuracy, and for an indefinite period. This capacity for the equilibration of its body without the possession of paired appendages is both remarkable and deserving of more careful study than has yet been given.

With the possession of a simple ear, the tubular portion of which lies in one plane of space, and with the lack of equilibrating paddles in the form of pectoral and pelvic appendages, Bdellostoma maintains its position while in motion with at least as great precision and as great apparent ease as any of the vertebrates possessing paired appendages.

It is clear, then, that it is not the necessity for the equilibration of the body that has brought about the development of the paired appendages in the vertebrate stock.

Since the formation of the paired appendages in all other water dwellers besides fishes is for the purpose of moving the body over the bottom, that is locomotion, it becomes very probable that the fish fin is a secondary structure, derived from the primitive pedal appendages, which were used by the ancestral form exclusively for locomotion.

This effectively disproves the theory of Gegenbaur of an ancestral archipterygium, and the Thatcher-Balfour lateral finfold theory, and it removes from the field of vertebrate morphology one of the most difficult problems which it has been called upon to solve, by simplifying the conditions of the problem.

While Bdellostoma is able to swim with ease, accuracy, and precision, and thus change its position in space either for the purpose of capturing prey, avoiding its enemies, or seeking a new position upon the bottom, it is not able to progress upon the bottom except by using the same swimming motion of its caudal region which enables it to progress through the water. It cannot

be said, however, to possess the power of locomotion except by swimming or springing. Undoubtedly the next step in the transformation of the Bdellostoma-like body of the ancestral Gnathostome was the gradual formation of pedal appendages, which enabled it to move easily, certainly, and symmetrically over the bottom.

It is just as erroneous to maintain any hypothesis which would derive the paired appendages of the Amphibia, for example, from the paired fins of fishes as it is to maintain the claim that the pectoral appendages (arms — forelegs) of land vertebrates are derived from the wings of birds.

When we consider the structure of the nervous system we are again brought face to face with the fact that amphioxus represents a developmental stage in the central nervous system repeated by other members of the vertebrate stock. Its nerve cord possesses all the relations to the other main organs of the body that are possessed by the central nervous system of other vertebrates. It lies immediately above the dorsal surface of the notochord in the hollow skeletal tube composed of a connective tissue membrane, in the walls of which, however, no chondroidal tissue is formed, and in which no calcareous matter has at any time been deposited, but this condition of the protective tube of the central nervous system is reproduced in the development of all the other vertebrates, from the amphioxus to man. This tube is not surrounded by skeletal structure in the amphioxus, but it is perforated with lateral openings made through its lateral face for the exit of the nerves passing out from it and entering it. In this it is also in harmony with the conditions found in all other vertebrates.

In the antero-posterior direction, the nerve tube is divided into two main parts, as in all other vertebrates, a brain and a spinal cord. While there are differences of histological value between the spinal cord of amphioxus and higher forms, this difference is hardly greater than exists between species of the higher vertebrates above it.

We may dismiss further consideration of this part of the nervous system with the statement that it is in every respect a vertebrate spinal cord. When we come to consider the structure of the brain, however, we find a simplicity in the arrangement of the

parts, which has until recently been an obstacle to most zoölogists in establishing the homologies between the amphioxus brain and the brain of the Craniata, and even to-day very few anatomists know enough about the structure of amphioxus to be able to establish the homologies which are existent.

Apparently the first zoölogists to note the presence of the amphioxus brain were Leuckart and Pagenstecker, who homologized the entire brain vesicle of amphioxus with four ventricles of the Craniata.

Owsjannikow later held the same view. In 1858, Professor Huxley, after careful examination, decided that the amphioxus neurocœle was the equivalent of the thalamencephalon of the Craniata.

In 1860, Wilhelm Müller concluded that it corresponded with the thalamencephalon and the prosencephalon of the Craniata. He further determined the location of the pigment in the anterior end of the brain tube and found that the pigment granules were located in the anterior ends of the brain cells. He also discovered that the olfactory pit was connected with the anterior end of the brain.

In 1861, Langerhans discovered the true relation of the olfactory epithelium of the olfactory tubercle of the brain. He decided that the amphioxus brain included the whole of the primitive Craniate brain.

In 1891, I described in a brief way some of the anatomical features of the amphioxus, giving the following account of the brain. "The anterior end of the neural axis of amphioxus is a brain and corresponds with a certain definite portion of the brains of other vertebrates. Its anterior wall is the homologue of the lamina terminalis of other vertebrate brains, and the anterior portion of its unpaired ventricle is the thalamocœle."

"I would define the vertebrate brain as follows: the 'vertebrate brain' is that portion of the anterior part of the axial nerve cord, associated with organs of special sense, containing an enlargement of the central canal, which is carried out into all structures formed by the outgrowth of the brain wall. Its walls contain the principal centers for the coördination of sensations and movements. All further additions to this simple brain (amphioxus) are made

in response to the demands of the organs of special sense, with which is associated extension of the coördination apparatus. With such additions we have the compound brain of all other known vertebrates up to man, inclusive."

"Reasons why the anterior end of the nerve cord of Amphioxus is a brain. It is a brain because: —

1. It forms the anterior termination of the neural axis.
2. It stands in intimate relation to the sense organs, eye, and nose.
3. It gives off at least two pairs of sensory nerves provided with peripheral ganglia.
4. It possesses large groups of ganglion cells forming centers of coördination.
5. It possesses an enlarged section of the central canal in the form of an unpaired ventricle with three well marked diverticula — two optic, one olfactory.
6. It is the largest part of the nervous system, at a time when the massive musculature and branchial apparatus of the anterior middle fourth of the body have not reached the stage requiring much enlarged central accommodations.
7. It shows in young larvæ growth to such an extent as to cause a ventral flexure of the chorda, while the brain itself bends downwards and so produces a "cranial flexure."
8. It shows in all other details of structure that *it is not* simply the *anterior end of the spinal cord*, but a *brain*.
9. It shows in a larval stage, soon after the differentiation of fibers in the neural axis (larvæ with one gill slit), a marked differentiation into ganglionic and fibrous regions, and the boundaries of the unpaired ventricle as well as of the lamina terminalis are distinctly marked out. There is then a ventricular segment of the brain reserved for the special sense organs. The fibers appear simultaneously with the formation of the pigment spot, and are in all probability the ways by means of which the sensations from this special sense organ are conveyed backward to the motor centers.
10. Since amphioxus is a vertebrate, these relations *must* have direct and important bearings on the phylogeny of the vertebrate brain and head, and will afford us invaluable aid in clearing up these intricate problems."

"The large collections of ganglion cells just posterior to the thalamocœle are homologous with the medullary nuclei of other vertebrates, since their connections show them to be centers for the control of the branchial apparatus, and the sensory and motor structures lying in the territory of the gill basket, *e. g.*, centers of respiration, deglutition, etc."

"The ontogenetic changes of the neural axis in other vertebrates carry the brain through the condition which in amphioxus remains permanent as the adult brain."

As regards the eye, I announced in 1891 that the eye-spot of amphioxus — that is to say, the unpaired but bilaterally symmetrical patch of epithelial cells lying in the lamina terminalis of the amphioxus brain — is the forerunner of the vertebrate eye, and that, as regards its physiology, it was not a visual organ nor an organ of sight, but an organ for the perception of the variations in the intensity of light.

This pigmented patch of epithelium occupies the same position in the adult amphioxus that the unpaired but bilaterally symmetrical patch of pigmented cells in the embryo sturgeon, as described by Kupffer, and in the embryo of Galeus, as observed by me, does with reference to the lamina terminalis of the brain of these forms.

In both the latter cases the pigmented patch is converted into the recessus opticus, and the recessus opticus gives rise by a process of evagination to the two optic vesicles.

Amphioxus, therefore, presents us with an adult condition which is represented in the higher vertebrate form by the simple condition of the brain wall in the earlier stages of the development of the nervous system.

For a fuller discussion of the anatomical conditions present in the adult amphioxus see my paper (*loc. cit.*, pages 238 to 234).

It is clear from this description of the lamina terminalis in the embryos of the sturgeon and of the dog-fish that the early stage of the eye in fishes is truly comparable, indeed is homologous, with the eye organ in amphioxus and is developed in identically the same way. As I have already pointed out, the pigment in the eye of the amphioxus lies in the inner end of the cells forming the anterior end of the neural tube.

In the sturgeon this pigmented area on the inner face of the

anterior brain wall is subject to the evagination process, being carried out with the cells of the recessus opticus.

My conclusions with reference to the eye of amphioxus were based upon a very extensive study of the eye of both the old and the young of amphioxus, and I was able to show that there is a great diversity in the form of the pigment area in different members of a series of individuals and that there is a tendency for the pigment area to divide symmetrically on either side of the median line.

Of greatest moment, therefore, are my observations and those of Kupffer which show that the pigment to be later used in the retina of the eye is first of all laid down in the inner ends of the cells of a primitively unpaired, even though bilaterally symmetrical, plate of cells which evaginates from the brain as the recessus opticus.

Minot attempts to homologize the vertebrate eye and optic tract with the highly differentiated arthropod eye, supra-esophageal ganglion and the circumesophageal nerve ring, but the idea that the visual organ of the vertebrates is to be sought for in such a specialized organ as the compound eye of arthropods is unsupported by morphological facts.

The nose in amphioxus remains in the form of a conical epithelial pit, whose apex is connected with or is in contact with the anterior end of the brain.

This pit is the so called sinus olfactorius impar, being the remains of the anterior neuropore. The right and left walls of this conical pit are thus morphologically equal, and, notwithstanding the fact that the pit is later pushed to one side by the growth of the base of the median fin-fold, we must hold that it is bilaterally symmetrical both in origin and in adult life and is strictly comparable to the plate of cells which evaginates from the anterior end of the brain of Bdellostoma and of the sturgeon, and which has been conveniently called the unpaired nasal plate.

It has long been accepted that the nasal epithelium of the Gnathostome vertebrate is laid down as a pair of bilaterally symmetrical plates in the embryo and continues paired throughout life, while in the Cyclostome it is laid down in an unpaired condition and ever remains so. Nothing could be more incorrect, for the plate in some Amphibia is identical with that in the Cyclo-

stomes. It is a single patch of cells symmetrically placed with reference to the sagittal plane of the body. In reality it is a double patch, although the indifferent tissue, which later forms a septum, has not at this stage developed.

It is said that in Acipenser embryos a median unpaired nasal plate precedes the paired nasal organ. This being the case, we have all the more reason to consider the Marsipobranch nose a paired structure, even though it appears to develop from an unpaired plate.

There is certainly no truth in Haeckel's dictum that "the pharyngo-nasal canal [of Myxinoids] is a secondary acquirement in connection with parasitic habit."

Notwithstanding that much has been said about the naso-pharyngeal tube of the Myxinoids, the full significance of this structure has not yet been made out. While it at first seemed to be an organ at the height of its development in Bdellostoma, the embryological evidence would indicate that it is a very old structure. We should not forget that in the Petromyzontes it is already closed off from the pharynx, and that in all other vertebrates it arises in a very early stage of embryonic life as a naso-hypophysial invagination of the ectoderm towards the mesenteron. It would thus seem to be on the verge of extinction in the Cyclostomes. No other stages of its development are known to us.

The total absence of an auditory organ in amphioxus is held by certain zoölogists to be a difficulty in the way of accepting this animal as an ancestor of the vertebrate stock.

They point out that in the tunicates, especially in the Appendicularia, there is an otocyst with inclosed otolith, which supposedly serves as an organ for the perception of wave motion in the water. It is also held that, since the tunicates stand in genetic relationship to the vertebrate stock, it is very unlikely that any form intermediate between them and the vertebrates would entirely lack an auditory organ. The error in their reasoning lies in the fact that they assume that the auditory organs of the tunicates and the vertebrates are homologous structures.

This is not the case, as all the evidence, both morphologic and ontogenetic, clearly proves. The vertebrate auditory organ is a neomorph arising within the vertebrate stock, from a sense-

organ rudiment entirely absent, so far as we yet know, from the tunicates. So that the absence of an ear from amphioxus is fully accounted for, at least in so far as relation to the tunicates is concerned. The tunicate ear is, in a strict sense, an otocyst, and not an ear.

With reference to the segmentation of the body of amphioxus, all the evidence seems to point to the ancestral character of this segmentation in relation to mesodermic segmentation of the higher vertebrate forms, with the exception of one peculiarity, which is probably palingenetic in its nature, but which, so far as we know, does not occur unmodified in any other vertebrate. I refer to the origin of the mesodermic segments from two bilaterally placed hollow pouches pushed out from the mesenteron.

From the many indications which have been discovered by numerous investigators, the mesoderm in the higher forms follows this plan of origin, but the architecture of the transformation is cœnogenetically very much shortened and changed, as in the case of many other organs of the body.

There is no occasion to dismiss all the pertinent indications preserved in the higher forms which indicate that this method of origin was the primitive one, simply because complete and well formed diverticula are absent from the ontogeny of the mesoderm in all vertebrates above amphioxus that have yet been investigated.

Regarding the suggested affinity between amphioxus and the annelids in this matter of the segmentation of the mesoderm, the unprejudiced mind will not hesitate to make the conclusion that it is far less intimate than the relationship already described.

The difficulties surrounding the establishment of the homology of the reproductive organs of amphioxus with those of the higher vertebrates are certainly not solved by any reference of the vertebrate stock to the annelids as ancestors, for the difficulty complained of by Minot that the reproductive organs appear segmentally in amphioxus, but non-segmentally in other vertebrates, is only increased by carrying the ancestral vertebrates back to the annelids, for here the segmental arrangement of the gonads is even more primitive and is accompanied by many annelidan characters of the other organs of the body; which carry us farther

than ever away from an explanation of the origin of the internal sexual organs of the vertebrate body. Certainly, when we have to choose between annelids and amphioxus for an ancestor of the vertebrates, it would be giving up much we have already gained to go back to the vermian type when we have an animal such as amphioxus, possessing many of the vertebrate characters already developed and showing a stage of organization which no one can for a moment doubt is immediately below that of the vertebrates and far removed from that of the annelids and tunicates. It is good occasionally for the zoölogist to view in the large and in perspective the whole animal and to take note of the interrelationship of all its parts, together; in other words, to take a "bird's-eye view" of the form being studied in order that minute and occasional differences, which our incomplete knowledge does not yet permit us to explain, shall not be unduly magnified and thereby be given an importance entirely unwarranted, and thus prevent our establishing the homologies and recognizing the real genetic relationships of the form in question. Much that has been said about amphioxus in recent years has been in the nature of zoölogical quibbling, a playing with non-essentials and an ignoring of the fundamental facts of the anatomy and development of this creature.

The intestinal tract of amphioxus also represents an ancestral condition, which is passed through ontogenetically by higher vertebrates. The liver pouch always arises as an unpaired diverticulum of the mesenteron, which later becomes established as a pair of diverticula higher up in the phylum.

As regards the other features of the intestinal tract, they remain in a very primitive condition, and in the Cyclostome we have a decided advance towards the condition occurring in higher forms. In the Cyclostome the liver becomes a massive gland, with the characteristic vertebrate structure, but neither amphioxus nor the Cyclostomes possess a pancreas.

The mouth in amphioxus is extremely primitive and shows no traces of skeletal structures which may yet be safely homologized with the maxillary and mandibular appendages of the Cyclostomes and the vertebrates above them.

The endostyle, which exists in a high state of development in amphioxus and which is well preserved in the larval Ammocœtes,

possesses as its function the collection and transference of food to the pharynx. During the transformation of larval Ammocœtes into the adult Petromyzon the organ is functionless. Beginning with the adult Cyclostome, and from there on throughout the rest of the vertebrate series, its remnant forms the thymus gland.

As regards the excretory organs of amphioxus, the researches of Boveri show that they are segmental in nature and that each tubule opens upon the surface of the body, no collecting duct being formed. Even on the theory of the annelidan origin of the vertebrates this is a stage of development through which the vertebrate ancestors must have passed, and instead of being an argument against the close genetic relationship of amphioxus to the vertebrates above it, it is one of the best examples we have in all zoölogy of the persistence of an extremely primitive condition of an organ, even after the general advancement of the body, in a morphological sense, makes the presence of such segmental organs appear out of place and not in harmony with the stage of development of the organism as a whole.

A similar instance of the persistence of primitive excretory organs in the adult condition is furnished by Bdellostoma, the only vertebrate which possesses a functional pronephros in the adult condition, and when we compare the adult pronephros of the Bdellostoma with the ontogenetic condition of the pronephros as seen in mammals and in birds, we recognize at once that the differences between these two stages are greater than the differences, for example, which we find between the mesodermic segmentation of amphioxus and other vertebrates or the segmentation of the reproductive organs of the same two forms.

So that this evidence, as well as all that I have previously brought to notice, points to amphioxus as the nearest living form among the ancestors of vertebrates.

A glance at the information contained in the table given below will serve as a basis for comparing Bdellostoma with amphioxus, on the one hand, and with the higher vertebrates, on the other.

Table of some of the primitive characters (p.) of Bdellostoma which are embryonic (e.), for higher vertebrates.

1. Notochord. (p. e.)
2. And its extension to the hypophysis. (p. e.)

3. Membranous skeleton of Bdellostoma. (p. e.)
4. Simple heart. (p. e.)
5. Cranial aorta. (p. e.) (Subcordal aorta.)
6. Peritoneo-pericardial cavity. (p. e.)
7. Subintestinal vein. Ventral vein of amphioxus. (p. e.)
8. Passage of subintestinal vein through liver without capillary net (p. e.) { Persistent subintestinal vein, which passes around portal system.
9. Gill arteries correspond to gill arches, not to hemibranchs. (p.)
10. Vein from pronephros to right cardinal vein. (p. e.)
11. Blood from anterior body walls passes into portal system. (p. e.)
12. Contractile portal heart. (p.)
13. Origin of carotids from lateral branchial commissure. (p. e.)
14. Segmental disposition of somatic and renal artery and veins. (p. e.)
15. Frequent anastomosis between post. card. veins. (p. e.)
16. Inferior jugular veins. (p. e.)
17. Large number of gills up to 14. (p. e.) { Functional branchial vessels; functional branchial bars or cartilages.
18. Their reduction during ontogenesis. (p. e.)
19. Functional pronephros. (p. e.)
20. Absence of genital ducts. (p. e.)
21. Brain. (p. e.)
22. Cranial and spinal nerves — separation of motor and sensory branches. (p. e.)

When we compare these characters of a Craniate with the conditions obtaining in amphioxus, we find a surprising agreement between them.

I think, from the presentation of facts just made, it is clear that amphioxus belongs to the ancestors of the present day vertebrates. It is, however, neither a Craniate nor a Gnathostome, and it is separated from all the other forms by a zoölogical gap which we cannot yet adequately measure, but which is very large. Let us now pass to a consideration of the relationships of the Craniate Vertebrata.

Let us assume, with Haeckel, that the Prospondylia are the stock from which the Leptocardia and the Archicrania both arose.

From the latter hypothetical group are developed all the Craniate forms which, down to the present time, have been classified in two main divisions: the Cyclostomata and the Gnathostomata.

In 1894, I showed that the so called tongue apparatus of the Cyclostome fishes, particularly of the Myxinoids, was developed by a transformation of the jaw apparatus from the maxillo-mandibular apparatus of some Gnathostome ancestor, and these views, together with the anatomical evidence supporting them, were printed in the *Journal of Morphology*, vol. 17, and in the *Bulletins* of the University of Cincinnati, vol. 1, nos. 1 and 2.

The development of the mouth of Bdellostoma and the pre-oral and postoral bars (the maxillary and mandibular arches) respectively in the early stages of Bdellostoma, before the formation of the tongue apparatus, adds further corroboration of the accuracy of the interpretation of the homologies of the cranio-facial apparatus of the Marsipobranchi.

With the discovery of the jaw apparatus in the Cyclostomes, the most essential character used by systematists for the separation of this group from the Gnathostomes disappears.

Many other characters, however, of which perhaps the absence of paired appendages is the most noteworthy and important, remain as a sufficient ground for a very distinct separation of these forms from the rest of the vertebrates.

But the group Gnathostomata must now include the Marsipobranchi as well as all the forms hitherto included, so that, as our classification now stands, *all* the Craniata are Gnathostomes, and, as before, the only living Acraniate is amphioxus.

The solution of the problem of the origin of the cranio-facial apparatus is thus pushed back upon the extinct vertebrate forms which fill in the gap between the common ancestor of amphioxus and Craniata. Possibly paleontology may bring us the needed information, or it may be that the embryology of some form yet unstudied will disclose the method of the transformation of the acraniate or agnathous into the craniate or gnathostome head.

Cincinnati, Ohio

OLD AGE IN BRACHIOPODA — A PRELIMINARY STUDY

H. W. SHIMER

THE following paper was prepared as the result of studies pursued at Harvard University under the direction of Professor R. T. Jackson, to whose oversight and suggestive criticisms the writer is indebted. Thanks are also due Mr. R. H. Willcomb of Ipswich, Mass., for his kindness in taking the photographs.

In this study we have made use of the fine collection of the Student Paleontological Department of Harvard University, the collections of the Boston Society of Natural History, and those of the Massachusetts Institute of Technology. Unless otherwise stated, the specimens referred to are in the Student Paleontological Laboratory at Harvard University. Those from the Massachusetts Institute of Technology are either still in that institution or have since been transferred to the Boston Society of Natural History.

This paper aims to summarize the principal characters which accompany old age in brachiopods, to illustrate them with some typical examples, and to present a few suggestions as to their origin and meaning.

Following the present usage, we employ the terms, nepionic for the larval or postembryonic stage of an animal's individual development; neanic for the immature or adolescent; ephebic for the mature or adult; and gerontic for the senile or old. Each one of these is further subdivided into three substages by the prefixes, ana-, meta-, and para-, denoting the beginning of a given stage, its culmination, and its decline (Hyatt, '94, pp. 390–397; '93, pp. 93–108).

SENILE CHARACTERS

Senility is expressed in the shell by one or more, frequently all, of the following characters:—

1. *Lamellosity of Growth Lines.*— The concentric growth lines become more closely spaced and lamellose, with a tendency to pile up at the lateral and anterior borders of the shell.

Examples: a pedicle valve of *Laqueus californicus* Koch, No.

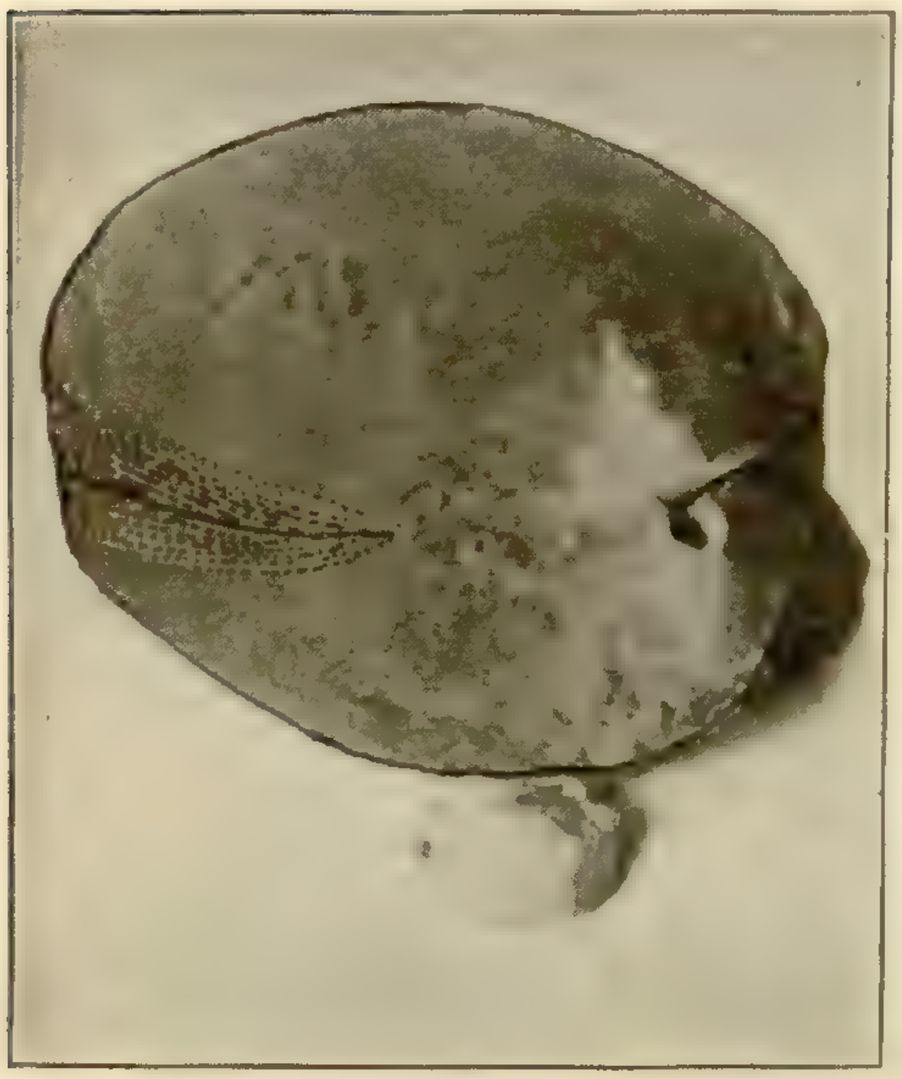


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FIG. 1.— A senile individual of *Laqueus californicus* Koch from Catalina Island, California. Old age is indicated by the lamellosity of the concentric growth lines on the gerontic portion of the shell and by the change there in the angle of curvature. The resorption of the umbo by the pedicle is likewise shown. No. 715, Harvard.

FIG. 1a.— A different view of the individual seen in Fig. 1, showing resorption of the umbo and of the deltidial plates by the pedicle.

715, up to and including its mature growth, a length of 40 mm., has only one or two strongly marked growth lines, while on its

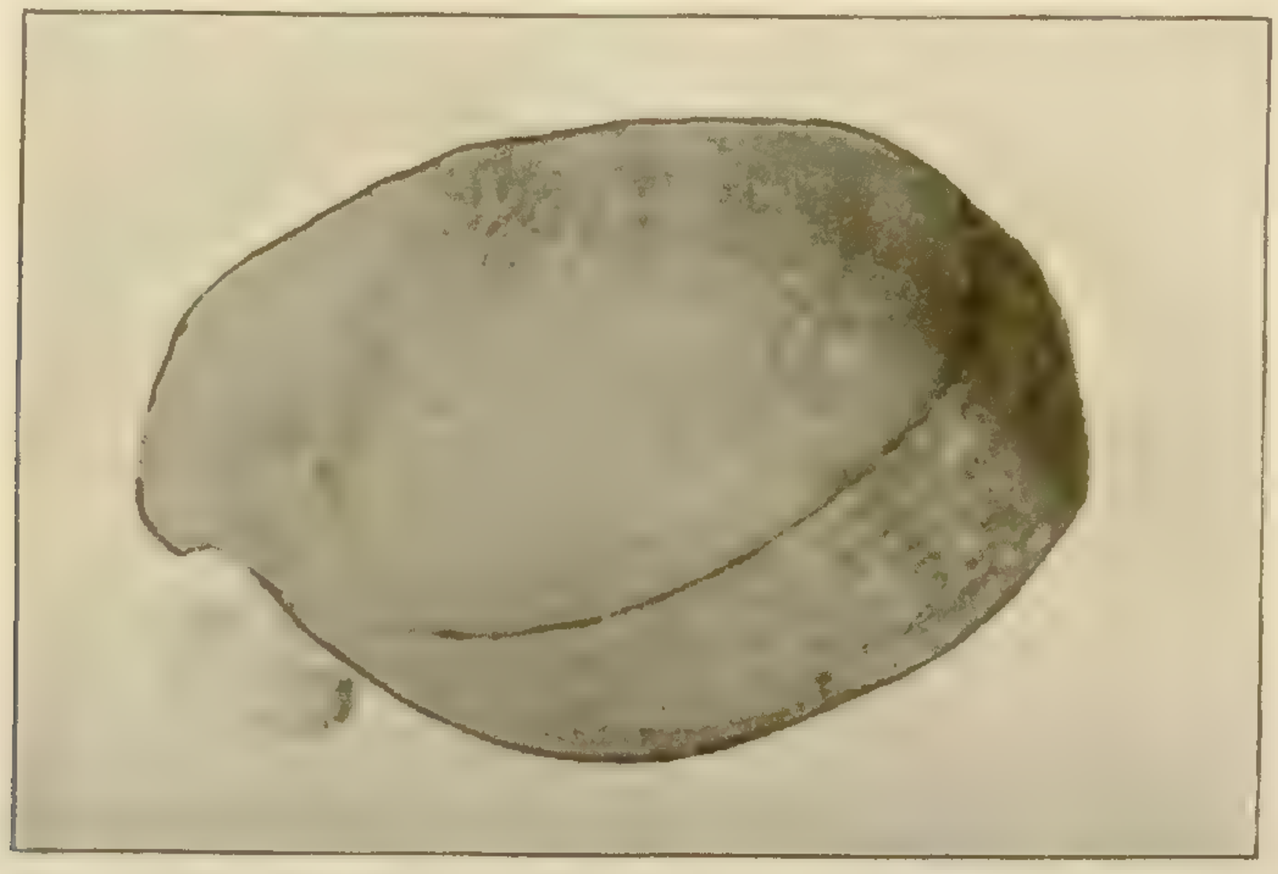

FIG. 2.— A side view of the individual seen in Fig. 1, showing anteriorly the change in the angle of curvature.

gerontic portion there are at least eight in a length of but 10 mm. (Figs. 1 and 2.)

A specimen of *Atrypa spinosa* Hall, No. 499, has in its mature or ephebic stage a length antero-posteriorly of 30 mm. or of 36 mm. measured on the curve of the pedicle valve. In succeeding growth originated a change in the angle of curvature at the anterior portion of the shell, indicating old age (see below). From the umbo up to and including the mature portion of the shell there are 24 well marked growth lines about equidistant; on the gerontic or deflected portion there are nine growth lines in a space of but 4.5 mm. Thus in old age the growth lines become crowded, as one occurs in every 0.5 mm., while in the previous growth one occurred in only every 1.5 mm. The piling up of the growth lines was caused by their continued production unac-

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FIG. 3.— A very large senile individual of *Atrypa spinosa* Hall from the Hamilton of Eighteen Mile Creek, New York, showing the change in the angle of curvature, the groove at the junction of the valves, and the lamellose condition of the growth lines upon the gerontic portion of the shell. No. 499, Harvard.

FIG. 4.— A fully mature individual of *Atrypa spinosa* Hall, on which none of the above gerontic features appear.

companied by any considerable growth of the shell in the anterior direction (Fig. 3).

A Lower Helderberg specimen of *Atrypa reticularis* (Linné), No. 641, shows 12 growth lines on the gerontic portion in less than 5 mm. This is after the abrupt deflection while the preceding portion of about 21 mm. in length also had only 12.

2. *Change in the Angle of Curvature.—This often results in a groove at the junction of the two valves.* An abrupt change in

direction occurs at the lateral and anterior borders of the shell so as to produce maximum growth almost or completely at right angles to the plane of separation of the valves. This change is frequently so great as to produce a reëntrant groove of greater or less depth at the junction of the valves, at the lateral and anterior portions of the shell. The groove results from the failure of each successive growth line to build out as far as the preceding one, and thus results in bending in the edges of the valves so that they meet in a depression.

Examples: in a pedicle valve of *Athyris spiriferoides* (Eaton), No. 498, the first lamellose growth lines appear after the shell has attained a length of 22 mm. and a width of 26 mm. At this period in growth the shell not only ceased to increase in width at the cardinal angles but actually decreased and so produced a groove

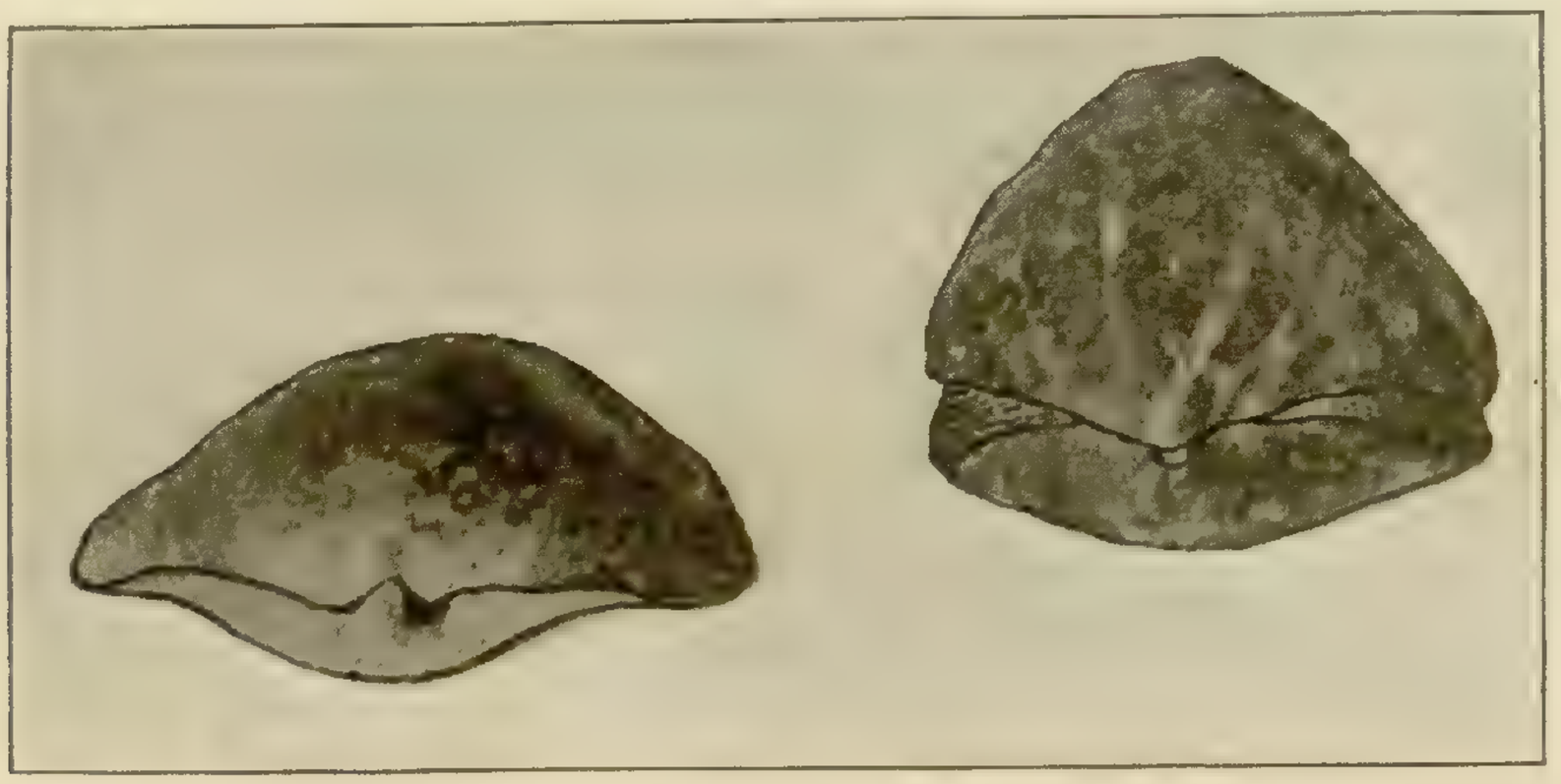

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FIG. 5.— *Athyris spiriferoides* (Eaton). A mature individual from the Hamilton group of Eighteen Mile Creek, New York.

FIG. 6.— A senile individual of *Athyris spiriferoides* (Eaton) from the Hamilton of Eighteen Mile Creek, New York. Gerontism is well shown here in the change in the angle of curvature and the conspicuous groove at the junction of the valves. No. 498, Harvard.

1 mm. in depth (Fig. 6). The change in the angle of curvature took place at the anterior portion of the valve later than at the cardinal angles.

In a specimen of *Laqueus californicus*, No. 715, measuring 45 mm. in length by 35 mm. in width, the change in the angle of curvature in old age at the sides of the shell is about 45°, and at the anterior portion is much less. This specimen also shows a shallow, broad groove at the cardinal angles (Figs. 1 and 2).

A slight groove is also developed at the cardinal angles of a

specimen of *Rhynchotrema capax* (Conrad), No. 142, and of *Atrypa spinosa* Hall, No. 499 (Figs. 8 and 3). In these specimens, however, the groove does not extend to the anterior portion of the shell as it does in some.

3. *Rotation of the Umbos toward Each Other.—This results in greater gibbosity of the shell.*

As shown above, the anterior growth of the valves in old age

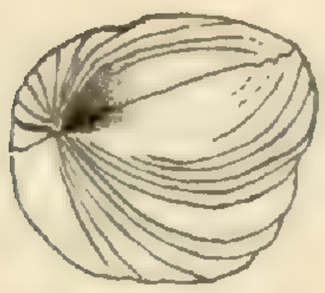

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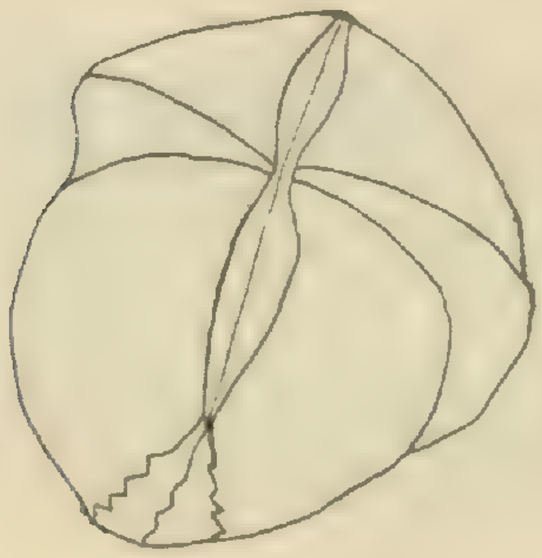
FIG. 7.— *Rhynchotrema capax* (Conrad) from the Hudson River group of Cincinnati, Ohio. A mature form.

FIG. 8.— A large senile individual of *Rhynchotrema capax* (Conrad) from the Hudson River group of Cincinnati, Ohio. Senility is shown in the lamellose growth lines and in the extreme gibbosity. No. 142, Harvard.

is at a more or less abrupt angle to the previous growth. This gerontic growth thus tends to push the edges of the ephebic shell farther and farther apart, and causes the valves to rotate outward on the axis of the hinge line. This rotation brings the umbos closer and closer together until often the beak of the brachial



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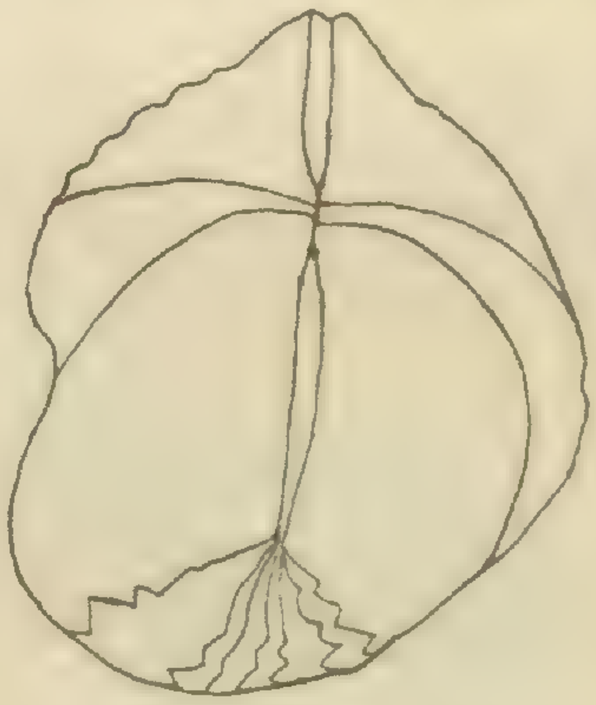

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FIG. 9.— A fully mature form showing in the pronounced growth varices the beginning of senility. *Platystrophia lynx* (Eich.) from the Hudson River group of Cincinnati, Ohio. No. 1910, M. I. T.

FIG. 10.— An advanced gerontic form of *Platystrophia lynx* (Eich.) from the Hudson River group of Cincinnati, Ohio. Old age is especially shown here in the strongly lamellose growth lines and in the closely approximated umbos. No. 1911, M. I. T.

valve encroaches on the delthyrium of the pedicle valve to such an extent as to block the original pedicle opening entirely (Figs.

8 and 10). As long as the pedicle remains active it will resorb the umbo of the pedicle valve as fast as the brachial umbo encroaches upon it, thus keeping a passage open for itself (Fig. 11). From this rotation of the valves there results a lengthening of the dorso-ventral axis of the shell. This gives it a gibbous appearance which is seen even in forms that are in maturity flat and thin, as *Rafinesquina alternata*. This great increase in thickness is shown in Figs. 3, 5, and 6, and also in the following measurements:—

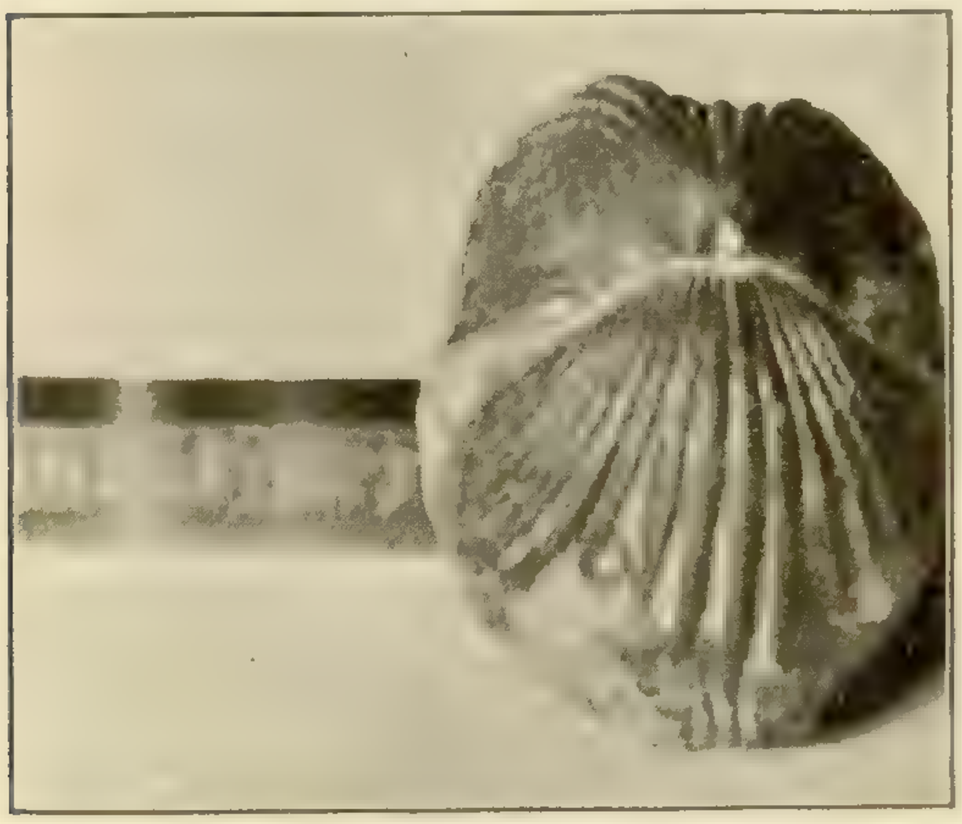

FIG. 11.— *Rhynchotrema capax* (Conrad). Hudson River group of Cincinnati, Ohio. A gerontic individual which has through resorption of the umbo, kept its pedicle passage open *pari passu* with the rotation of the umbos toward each other. No. 1156, Harvard.

Rafinesquina alternata (Figs. 12 and 13). Adult, No. 1912, M. I. T. Length, 32 mm.; breadth, 41 mm.; thickness, 3.5 mm. Old age, No. 128. Length, 39 mm.; breadth, 51 mm.; thickness, 11 mm.

Rhynchotrema capax (Figs. 7 and 8). Adult, No. 1913, M. I. T. Length, 22 mm.; breadth, 21 mm.; thickness, 26 mm.

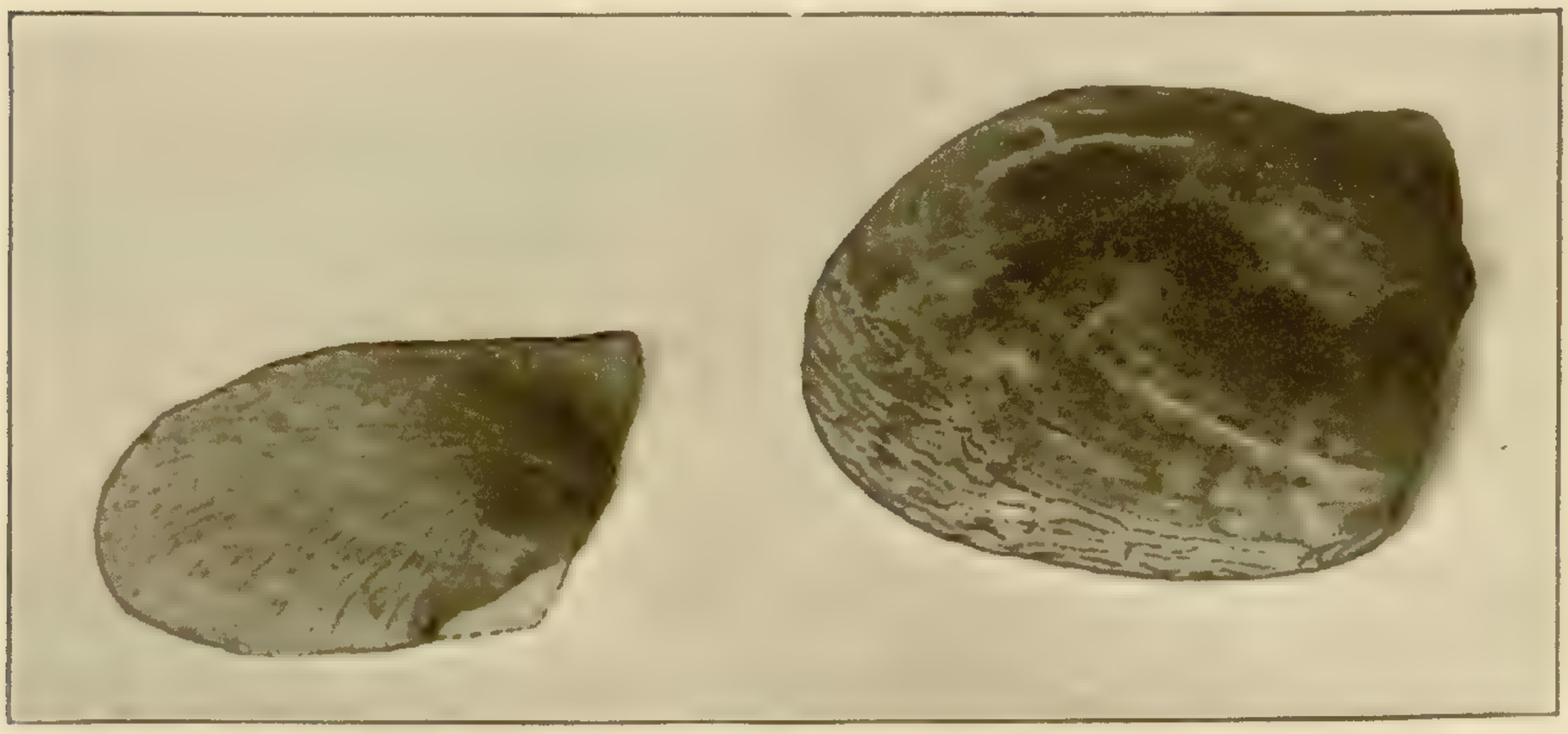

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FIG. 12.— Mature individual of *Rafinesquina alternata* (Emmons) from the Hudson River group of Cincinnati, Ohio.

FIG. 13.— A large gerontic individual of *Rafinesquina alternata* (Emmons) from the Hudson River group of Cincinnati, Ohio, indicating senility in the lamellosity of the concentric growth lines, in the changed angle of curvature, and in the greater gibbosity of the shell. No. 128, Harvard.

4. *Flattening-out of Plications.*—In old age the plications (ribs) tend to flatten out and disappear. Their presence is usually indicated on the gerontic portion of the shell by zigzag lines of growth, though the surface of the shell is at this area smooth. This is seen in *Rhynchotrema capax*, *Platystrophia lynx*, *Tropidoleptus carinatus*, Spirifers, etc., and holds true in all specimens examined (see p. 117).

Examples: in *Rhynchotrema capax*, No. 142, from Cincinnati, Ohio, the pedicle valve has during maturity 15 ribs; during metagerontism it has 11, and at the last growth before the death of the animal there are none, although zigzag growth lines represent them. The brachial valve has during maturity 14 ribs; during metagerontism, 10, with none at the death of the animal.

In *Spirifer oweni*, No. 57, from the Hamilton of Clark Co., Indiana, the ribs become broader and lower until in extreme old age they, as well as the zigzag growth lines at the edge of the shell, have almost entirely disappeared even at the anterior portion of the shell (see p. 117 for further discussion).

The ribs disappear earlier and more completely from the brachial than from the pedicle valve. This was noticed especially in *Terebratella plicata* Say, *Tropidoleptus carinatus* (Conrad), *Meekella striatocostata* (Cox), *Spirifer mucronatus* var. *thedfordense* Shimer and Grabau, and *Rhynchotrema capax* (Conrad). This character is often only faintly marked; its presence is first noted at the cardinal angles. Raymond (:04, p. 128), also notes the more nearly complete obliteration of the plications on the brachial valve in *Tropidoleptus carinatus*.

FIG. 14.—A gerontic individual of *Ambocœlia umbonata* (Conrad) from the Hamilton group of Eighteen Mile Creek, New York, showing the disappearance of the median sinus.

5. *Disappearance of Median Sinus and Fold.*—The median sinus and fold tend to flatten out and disappear in a few observed species.

Examples: in *Ambocœlia umbonata* (Conrad) (Fig. 14), the median sinus disappears in old age. In *Bilobites varicus* (Conrad) there is also a tendency to obliterate the marginal sinus. This is shown in a series of shells, No. 4, from the Lower Helderberg of Clarksville, Albany Co., New York (Fig. 15). For further examples see also Beecher (:01, p. 403).

In some species the median sinus appears to become more accentuated with age. For example, *Athyris spiriferoides* shows well this accentuation of the sinus with hardly any corresponding development of the median fold, while in *Cœlospira grabaui* Shimer, both sinus and fold are developed (Shimer, :04, p. 253).

FIG. 15.—Series showing gradual obliteration of the sinus from maturity to old age. *Bilobites varicus* (Conrad) from the Lower Helderberg of Clarksberg, New York. No. 4, Harvard.

6. *Enlargement of Cardinal Angles.*—The cardinal angles, that is, the angles made at the cardinal extremities between the hinge line and the sides of the shell, enlarge during senescence.

Examples: a specimen of *Rafinesquina alternata*, No. 128, has just preceding senescence, a cardinal angle of 87°. This increased to 99° during old age (Fig. 13).

A specimen of *Spirifer mucronatus* var. *thedfordense*, No. 405, has at the close of the neanic or *Spirifer mucronatus* stage (Shimer and, Grabau, :02, p. 171) a cardinal angle of 25°. This angle rapidly increases as seen in Fig. 16, through the ephebic and gerontic stages until it measures 60° at the death of the animal.

7. *Reduction of Shell Index.*—The shell index, *i. e.*, the breadth divided by the length, becomes smaller with old age (see Cumings, :03, p. 3). In other words the shell becomes proportionally longer in old age than in maturity and in this respect approaches the nepionic condition.

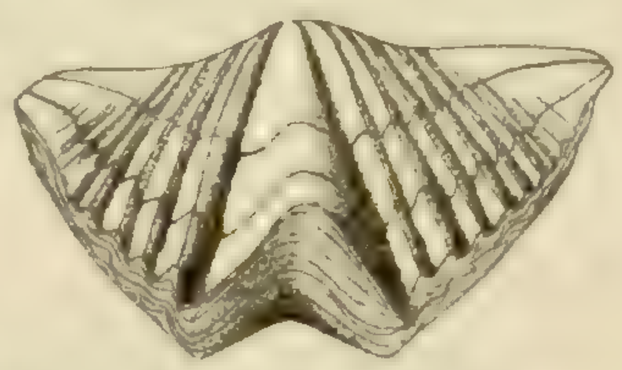


FIG. 16.—A senile form of *Spirifer mucronatus* var. *thedfordense* Shimer and Grabau, from the Hamilgroup of Arkona, Ontario. This shows senility in the enlarging cardinal angles and in the piled-up growth lines. No. 405, Harvard.

Examples: a specimen of *Spirifer mucronatus* var. *thedfordense* has during its nepionic stage a shell index of 1.77; during its neanic, 3.57; and during ephebic, 1.90. For further measurements and discussion of the varietal form see Shimer and Grabau (:02, p. 174).

An old specimen of the above species, No. 405a, had during early maturity a width of 34 mm. and a length of 14 mm., giving a shell index of 2.43. In old age the width was 33 mm., the length 18 mm., and shell index 1.83.

Rhynchotrema capax, No. 142, had in maturity a width of 18 mm., a length of 17 mm., giving a shell index of 1.06. In old age the width was 20 mm., the length 23 mm., and shell index 0.87 mm.

In *Rafinesquina alternata*, No. 128, the mature shell measured 42 mm. in width, 30 mm. in length, and the shell index was 1.40; the senile shell was 51 mm. wide by 39 mm. long with a shell index of 1.30.

8. *Modification of Pedicle Opening.— a. The pedicle opening may be enlarged during growth.* As the animal increases in size the pedicle normally increases in diameter if it continues attached. The resulting growth of the pedicle may resorb the surrounding shell (the deltidium or deltidial plates and umbo) and thus enlarge its opening. This is especially conspicuous in the Terebratuloids. In some shells resorption is made doubly necessary if the pedicle would continue to exist, for the rotation of the umbos toward each other would otherwise soon cut it off. This condition is seen well in some specimens of *Rhynchotrema capax*.

Examples: a specimen of *Laqueus californicus*, No. 715, is a senile individual as indicated by its lamellose growth lines, abrupt deflection, and groove at the cardinal angles. The umbo shows considerable resorption as do also the deltidial plates (Figs. 1 and 1a).

A senile specimen of *Hebertella occidentalis* Hall, No. 2, has a triangular delthyrium 9 mm. high, 5.5 mm. wide at the hinge line, and 2.5 mm. at the apex of the umbo. The delthyrium, already large in maturity with the deltidium resorbed, has been much enlarged in old age; in addition the umbo of the pedicle valve has been resorbed, destroying much more than the nepionic shell (Fig. 17). This destruction of the umbo may be partially due to breaking as shown by an irregularity at the anterior side, but there is no doubt that most of the opening is due to resorption

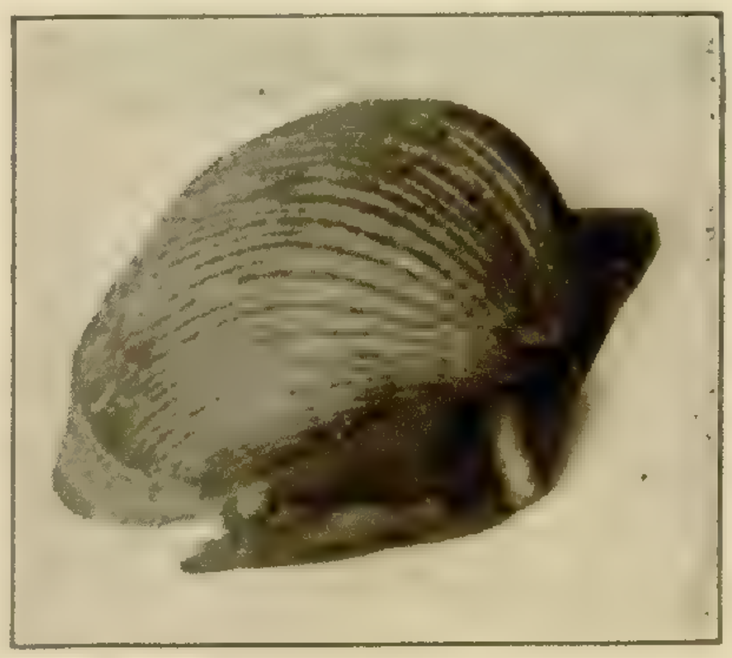


FIG. 17.— A subgerontic individual of *Hebertella occidentalis* Hall from the Hudson River group of Cincinnati, Ohio, showing the pedicle opening much enlarged through resorption of the umbo. No. 2, Harvard.

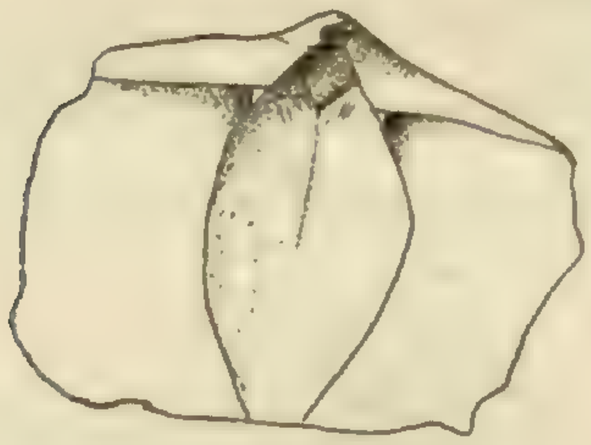
as it has the same general smoothness and evenness of the sides as the delthyrium.

In those forms of *Rhynchotrema capax* which continue attached throughout life, the increasing gibbosity makes necessary, even during late maturity, a resorption of the umbo of the pedicle valve. But this resorption becomes very great in senile specimens, as for example in a specimen, No. 1156, the apex of whose pedicle valve has been resorbed anteriorly at least 1.5 mm. (Fig. 11). The smoothness of this opening and the evenness with which it is prolonged out from the interior of the shell show it to result from true resorption and not from breaking.

b. The pedicle opening may be partially or completely closed. This is accomplished:—

(1) By deposits of calcareous matter in the apex of the valve, sometimes forming a callosity.

Example: in *Stropheodonta demissa* (Conrad), No. 1914, M. I. T., the delthyrium has been completely closed by growths that extend from either side and meet in the middle; these form two



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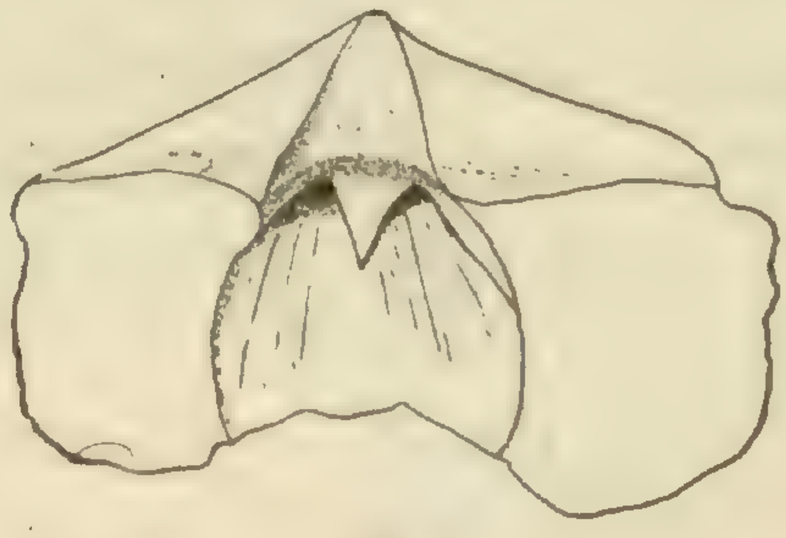

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FIG. 18.— The interior of the pedicle valve of a mature form of *Spirifer acuminatus* (Conrad) from the Upper Helderberg of the Falls of the Ohio, showing the beginning of the callosity in the pedicle cavity.

FIG. 19.— The interior of a pedicle valve of a gerontic individual of *Spirifer acuminatus* (Conrad) from the Upper Helderberg of the Falls of the Ohio, showing the accentuation of the callosity. No. 646, Harvard.

convex callosities on the inner or proximal side which meet in the median line. The outside of these growths is smooth and also the cardinal margin is wanting in the denticulations characteristic of the rest of the shell.

A testaceous callosity sometimes forms in the pedicle cavity, and extends across the delthyrium (see also Hall and Clarke, '94a, p. 6). This is seen in *Spirifer acuminatus* (Conrad), *S. granulosus* (Conrad), and *S. audaculus* (Conrad).

Example: in a gerontic pedicle valve of *S. acuminatus*, No. 646, the callosity extends 17 mm. from the apex of the valve to the anterior border, uniting the dental lamellæ and sending off a median portion forward between the posterior extremities of the diductor muscle impressions. In a mature valve of this species there appear only faint indications of this callosity in the apex (Figs. 18 and 19). Hall and Clarke ('94a, p. 921), mention this deposit of calcareous matter in the apex of the valve as a frequent condition in senile Spirifers. They also state that "the tendency to contract the pedicle cavity and deltidium presents its extreme manifestations in the Devonian forms of Stropheodonta, Strophonella and Leptostrophia where it has become almost and sometimes quite obliterated and the entire umbonal area filled with testaceous secretions" (Hall and Clarke, '94a, p. 919).

(2) By the encroachment of the umbo of the brachial valve upon the delthyrium of the pedicle valve, so as partially or completely to cover it. This follows from the rotation of the umbos toward each other in senescence as already described (p. 99). When its original opening is thus covered, the pedicle may keep its passage free by resorption into the umbo of the pedicle valve, as already seen (Figs. 1, 11, 17), or may become atrophied and disappear, leaving the shell unattached.

Examples: in a senile specimen of *Platystrophia lynx*, No. 1911, M. I. T., the umbos are so closely appressed that no pedicle opening can be seen (Fig. 10). An approach to this condition is seen in many senile Spirifers, *Rhynchotrema capax*, etc.

9. *Disappearance of Spines, Nodes, etc.*— In old age the surface tends to become smooth, thus repeating the nepionic surface character. In all forms this is noted first at the angles and later at the anterior portion of the shell. There is slight development of surface ornamentation among the brachiopods beyond the simple plications and median sinus and fold. This lack is especially noticeable when we compare this class with the pelecypods, gastropods, and cephalopods which are often characterized by an excessive development of ribs, spines, nodes, etc. If, in brachiopods, spines or nodes are present in maturity, they gradually become less numerous until in extreme old age they disappear entirely (see also Hyatt, '89, p. 20, and Beecher, :01, p. 94). Examples are noted in Productus, Atrypa, and Ambocœlia.

Productus horridus, No. 600, 43 mm. wide and with a length of 82 mm. following the curve of the pedicle valve, has no spines on the last added 12 mm. of the anterior portion, while the spines had disappeared earlier from the surface at the cardinal angles (see p. 110).

Another specimen of the same species, No. 607, has no spines on the last added 18 mm. This disappearance of spines in old age is also well seen in *Ambocœlia spinosa* and in *Atrypa spinosa*. In *Atrypa nodostriata* the disappearance of nodes from the senile portion of the individual was noted.

10. *Thickening of Valves.*—This may result in the formation of an elevated ridge about the muscular area and in the building of a ridge just inside the margin of the concave valve in concavo-convex forms. Both valves, and especially the pedicle valve, thicken by interior additions. The area of maximum increase usually extends from each side of the muscular impression to the cardinal angles. Sometimes, as for example in *Athyris spiriferoides*, the greatest thickening is at the lateral edges of the valves. The pedicle valve becomes especially thickened over the gential organs as seen in Atrypa, Spirifer, etc.

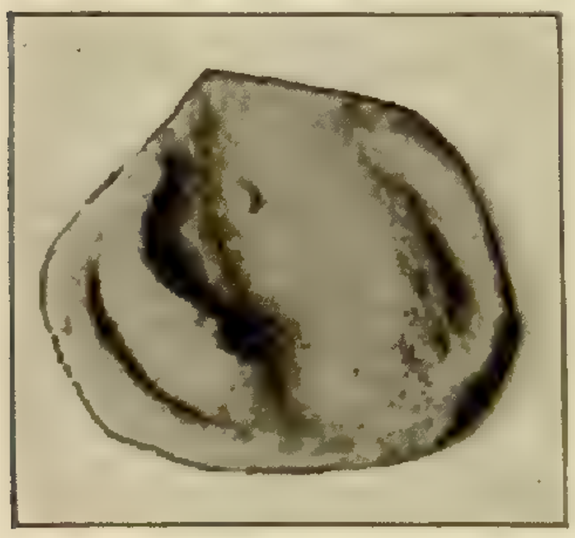

FIG. 20.— The pedicle valve of a gerontic specimen of *Atrypa reticularis* (Linné) from the Lower Helderberg near Catskill, New York. Old age is shown by the greatly thickened and inflected edge of the shell and in the prominent ridge bounding the muscular area. No. 641, Harvard.

Examples: a pedicle valve of *Atrypa reticularis*, No. 641, has a broad, prominent ridge bounding the muscular area laterally and sloping outward to a depression between it and the much thickened and inflected edge of the shell; it disappears entirely anteriorly (Fig. 20).

A pedicle valve of *Spirifer acuminatus*, No. 646, shows a greatly depressed muscular area due to the great thickening of the posterior portion of the valve on each side of it, which slopes gradually to the lateral margins of the valve (Fig. 19).

In *Platystrophia lynx*, No. 3, the pedicle valve is thickened very much at the sides of and anterior to the muscular area (see also Cumings, :03, p. 28).

In the above cases, as well as in all observed, the greatest thickening in the interior of the valve occurs in the region of the principal trunks of the vascular sinuses, and it is in these main trunks that in modern brachiopods the genital organs occur (for further discussion see p. 117). In most concavo-convex and resupinate shells the concave valve bears just inside its margin and posterior to where the convex valve fits over it, a swollen and strongly papil-

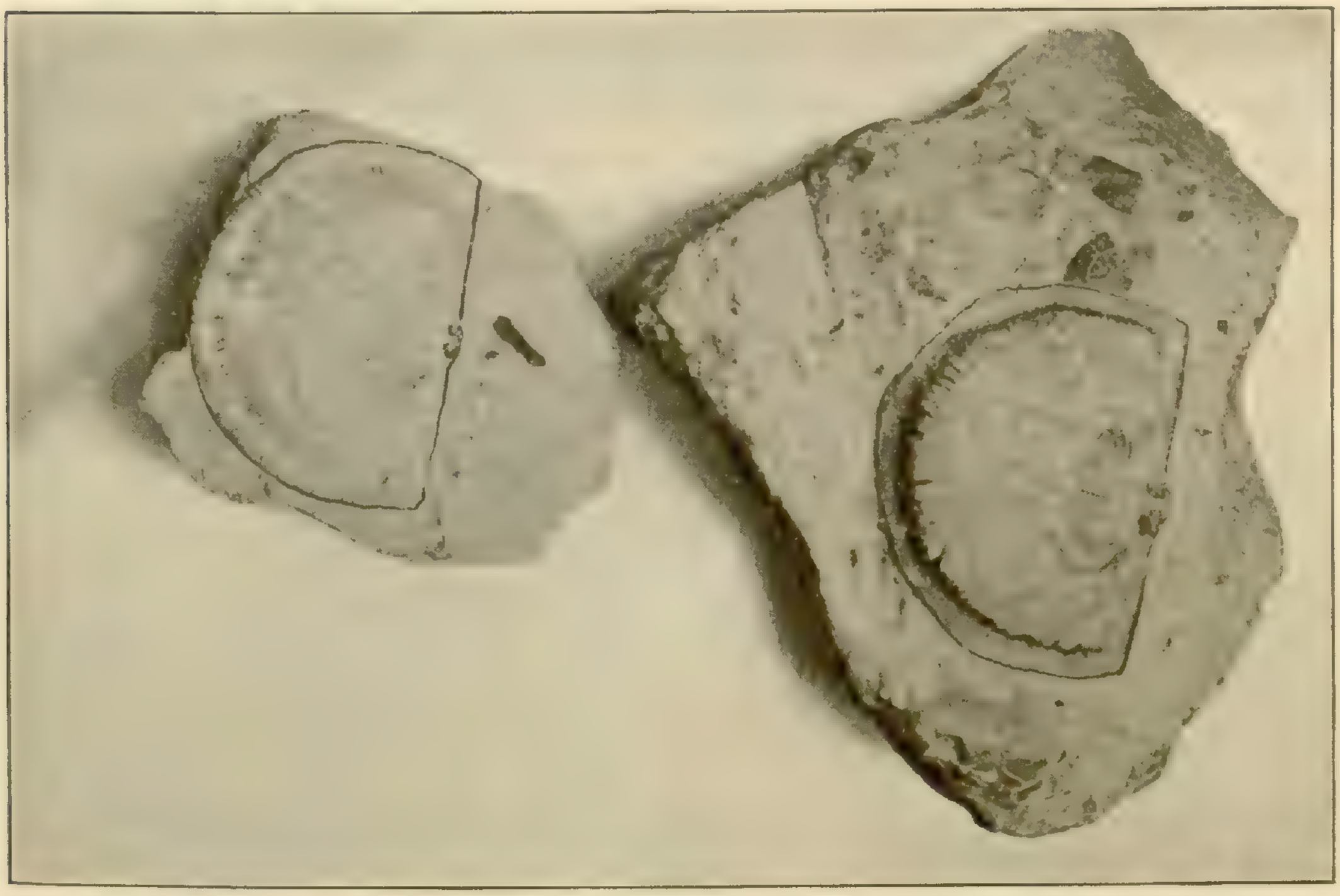

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FIG. 21.— A mature brachial valve of *Rafinesquina alternata* (Emmons) from the Hudson River group of Cincinnati, Ohio. No. 1, Harvard.

FIG. 22.— The brachial valve of a gerontic individual of *Rafinesquina alternata* (Emmons) from the Hudson River group of Cincinnati, Ohio, showing the vascular tumid ridge and its abrupt descent to the edge of the valve. Harvard collection.

lose ridge which extends from the cardinal angles to the anterior portion of the shell. In the brachial valve of *Rafinesquina alternata* the ridge has a very irregular surface and descends abruptly to the narrow margin of the valve. This makes the interior of the valve quite flat while the outside is concave (Fig. 22). This submarginal thickening was also noted in *Tropidoleptus carinatus* (Conrad), *Strophomena rugosa* Blainville, *Plectambonites sericeus* (Sowerby), *Chonetes granulifera* Owen, *Stropheodonta magniventra*

Hall, and *S. concava* Hall. Sometimes the papillæ are so well developed that they are spine-like. This was most conspicuous in *Stropheodonta magniventra*, No. 1165, and in *S. concava*, No. 1099, M. I. T.

In the majority of brachiopods the muscular area of the pedicle valve becomes in gerontic individuals depressed below the general interior level of the shell through the thickening of the shell about it, and thus frequently leaves this area translucent in its thinness while the remainder of the shell is very thick. The area is often strongly marked off from the rest of the valve by an elevated ridge at times high and well defined, surrounding it. This ridge is

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FIG. 23.— The pedicle valve of a mature specimen of *Hebertella occidentalis* Hall.
FIG. 24.— The pedicle valve of a gerontic individual of *Hebertella occidentalis* Hall, showing the high ridge defining the muscular area.

conspicuous in *Rafinesquina alternata*, *Leptæna rhomboidalis*, *Hebertella occidentalis* (Fig. 24), *Eatonia peculiaris*, and *Hipparionyx proximus*, in all of which the muscular area is strongly marked off from the rest of the shell. In *Spirifer acuminatus* (Fig. 19) the ridge surrounding the muscular area is merged with the general thickening of the shell. We have not been able to examine any senile forms in which the dental lamellæ of the pedicle valve are strongly developed and form a spondylium, as for example in Pentamerus, Gypidula, etc. In these the muscular area is thus raised instead of retaining its youthful position. This thickening of the valves may in a few individuals result in the lessening of the total capacity of the body chamber. Usually,

however, the internal thickening is more than offset by the growth of the margins of the valves toward each other; for even a slight marginal growth means a large increase in the cubic capacity of the shell.

Descriptions of a few Species

The following species were chosen for description of senescence because there were gerontic specimens of them in the collections studied and also because they are common. Similar old age characters were, however, noted upon all forms which showed any approach to gerontism. When one specimen is described, this is merely taken as a type but the characters hold true for all the specimens of that species examined.

Rafinesquina alternata (Emmons).— A large specimen, No. 128, from the Hudson River group of Cincinnati, Ohio, was 30 mm. long when it first showed signs of old age in the appearance of lamellosity and in the changed angle of curvature; this change is much more noticeable on the pedicle than on the brachial valve. The shell also increases in thickness from 3.5 mm. in a normal mature specimen to 11 mm. in this gerontic individual. In old-age specimens of this species the pedicle opening is usually entirely closed and if it exists, is much too small to admit the passage of a pedicle large enough to support a shell of such a size (on this point see also Hall and Clarke, '92, p. 141). This condition is not, however, due wholly to senility but existed during maturity.

The interior of the brachial valve has, extending from the cardinal angles around the margin of the valve anteriorly, a tumid ridge with a very irregular surface. This descends abruptly to the edge of the valve. For comparison of mature and gerontic forms see Figs. 21 and 22.

Strophomena rugosa Blainville (*Streptorhynchus planumbonus* Hall).— A pedicle (concave) valve, No. 582, of this species bears just inside its edge a tumid ridge with a considerable vascular surface, which is not developed to such an extent as in the concave (brachial) valve of *Rafinesquina alternata*. This fact is interesting as the ridge is developed in opposite valves in the two species. The muscular area remains translucent while the rest of the valve

becomes much thickened and more or less grooved by vascular markings. Both valves of this species bear lamellose growth lines. There is also a greater lamellosity in the latest built portion of the deltidium and chilidium.

Productus horridus Sowerby.— No. 600 from the Lower Zechstein of Gera, Thuringia, is not very senile. Old age, however, is indicated by the greater concavity of the brachial valve and by the absence of spines from the last added 12 mm. of the anterior portion. They had disappeared before this from the cardinal angles, showing thus the progressive advance of senility from the cardinal angles to the anterior portion. This order of disappearance is just what we should expect from their order of initiation, appearing as they do at the cardinal angles before they develop on the main portion of the shell.

Platystrophia lynx (Eichwald).— A gerontic individual of this species from the Hudson River group of Cincinnati, Ohio, No. 1911, M. I. T., attained a length of 31 mm. before it began to show evidence of old age in any marked degree; after this point it added a length of 13 mm. to each valve. The senescent characters noted here are: lamellosity of growth lines, flattening of the ribs, and formation of a groove at the cardinal angles. Through the change in the angle of curvature and the consequent growing toward each other of the two valves, the entire shell becomes very gibbous. The accentuation of these characters in increasing old age may be seen by comparing Figs. 9 and 10. The cardinal angle measures 78° at the close of the ephebic stage and 94° in the gerontic. Similar observations are given by Cumings (:03, p. 12).

A pedicle valve of this species, No. 3, from the Hudson River group of Cincinnati, Ohio, shows a very pronounced thickening on each side of and anterior to the muscular area. This area thus appears to be very much depressed, with high, perpendicular bounding walls. The development and relationship of this species are very thoroughly discussed and illustrated by Cumings (:03).

Rhynchotrema capax (Conrad).— A specimen of this species, No. 142, from the Hudson River group of Cincinnati, Ohio, after reaching maturity when it had a length of 15 mm., became lamellose at the cardinal angles and the ribs began to flatten out, while the angle of curvature in each valve became relatively greater.

It then lengthened the pedicle valve 8 mm. on the curve of the shell, during ana- and metagerontism. At this point the growth lines become still more lamellose, more of the ribs flatten out, and a sudden increase in the angle of curvature takes place. From this point it added 7 mm. to each valve. There is shown especially on the median sinus and folds of this latest added portion a groove in the center of each rib on account of the changed plane of growth. A shallow groove is formed at the junction of the valves. This is greater at the cardinal angles since it is there first formed and proceeds progressively anteriorly. This groove is due in the anterior portion to the last added two or three growth lines only. The specimen has the pedicle opening entirely filled by the umbo of the brachial valve. Another specimen, however, No. 1156, as large as the preceding and representing a similarly advanced stage of senescence, has a very large pedicle opening. Mature and gerontic forms are shown in Figs. 7 and 8.

FIG. 25.—A senile individual of *Tropidoleptus carinatus* (Conrad) from the Hamilton group of Eighteen Mile Creek, New York. Old age is indicated in the enlargement of the cardinal angles, reduction of shell index, and in the flattening-out of the ribs. These last always disappear progressively from the cardinal angles to the front of the shell. No. 1915, M. I. T.

Terebratula harlani Morton.—In this species old age is shown in the lamellose concentric growth lines, the change in the angle of curvature, the groove at the cardinal angles, the larger cardinal angle, and the resorption of the umbo and deltidial plates. Exactly similar characters are shown in *T. perovalis* Sowerby.

Tropidoleptus carinatus (Conrad).—In an old-age specimen of this species, No. 1915, M. I. T., the ribs are flattened out on the gerontic portion and the growth lines are lamellose, irregular, and more or less piled up. These senile characters appear progressively from the cardinal angle to the front of the shell (Fig. 25). The cardinal angle enlarges and the shell index grows smaller. The ribs flatten out on the brachial valve before they do on the pedicle valve. In other specimens the submarginal ridge of the concave (brachial) valve, so characteristic of *Rafinesquina alternata*, also occurs, though in a less marked degree. Raymond (:04, pp. 126–131) discusses this species fully.

Laqueus californicus Koch.— A specimen of this recent species, from Catalina Island, California, No. 715, shows old age in the lamellose growth lines, the change in the angle of curvature, and the formation of a groove at the cardinal angles, and in the larger cardinal angles (Figs. 1 and 2). These characters also appear in *L. rubellus* Sowerby, etc.

Atrypa spinosa Hall.— In a specimen from the Hamilton of Eighteen Mile Creek, New York, No. 499, old age is first indicated after a growth of 27 mm. by the sudden crowding together of the growth lines and by the change in the angle of curvature. After this the anterior growth through the change in curvature adds about 5 mm. to the thickness of the shell and 4 mm. to its length measured along the antero-posterior axis. This gives the shell a very gibbous appearance. Senility is first expressed at the cardinal angles as seen in the development there first of the greater lamellosity of the growth lines, the change in the angle of curvature, and the formation of a groove which does not extend far anteriorly. The thickness of the comparatively flat pedicle valve is much greater than that of the brachial. For comparison of the senile characters of this specimen with an adult form, see Figs. 3 and 4. A pedicle valve, No. 641, shows the separation of the muscular area from the rest of the valve by a thick, prominent ridge which is especially developed at its sides, *i. e.*, over the genital organs (Fig. 20). The thickened lateral edges of this form a prominent inflected edge.

Spirifer mucronatus var. *thedfordense* Shimer and Grabau.— A specimen of this species, No. 405, from the Hamilton group of Arkona, Ontario (Fig. 16), shows old age in an increase of the lamellosity of the concentric growth lines, the fading-out of the ribs, the change in the angle of curvature, and the development of a groove cardinally at the junction of the two valves. These characters hold true in all senile specimens of this genus examined. In *S. acuminatus* the greatest thickening of the valves is on each side of the muscular area. This character appears to hold true in all species. In some species (*e. g.*, *eurytcines*, *acuminatus*, *oweni*, etc.) a conspicuous thickening (callosity) occurs also posterior to the muscular area in the pedicle valve, thus separating it widely from the apex of the valve (Fig. 19).

Nucleospira ventricosa Hall.—Senility in this very small, Lower Helderberg species is shown by a conspicuous roughness or lamellosity of the concentric growth lines in the otherwise smooth shell, a change in the angle of curvature, and the formation of a reëntrant groove at the cardinal angles, the point where senility is first indicated. No shell sufficiently senile to have developed a groove in the anterior portion was observed.

Athyris spiriferoides (Eaton).—One specimen from the Hamilton of Eighteen Mile Creek, New York, No. 498, was 22 mm. long and 26 mm. wide when senescent characters first appeared. After that it grew 10 mm. anteriorly measured on the curve of the shell. This growth increased the antero-posterior axis only 6 mm. The maximum width of the pedicle valve was increased only 2 mm. though the total amount added to the width in old age measured over the curve of the valves, was 11 mm. The rest of the growth both anterior and lateral merely added to the thickness of the shell. In this shell old age is expressed by the lamellosity of the growth lines and the change in the angle of curvature. This latter character is more especially noticed at the sides of the pedicle valve as this valve piled up growth lines here to a thickness of 4.5 mm. The lateral edges of the brachial valve thickened less. A groove was formed at the junction of the valves. The cardinal angle enlarged from 100° in the mature shell to 125° in parageröntism (Fig. 6). This specimen shows the normal progression of old age characters from the cardinal angles to the anterior border, in the first appearance there of the lamellose growth lines and of the groove. This groove at the death of the animal had advanced only halfway to the anterior border of the shell. A separate pedicle valve, No. 635, shows the maximum thickening from each side of the muscular impression to the cardinal angles, with the greatest thickening at the edge of the valve. Figs. 5 and 6 show for comparison a mature and a gerontic individual.

Conclusions.

Minot ('91, p. 151) says very suggestively: "I think it is now conclusively established that there is in guinea pigs a progressive

loss in the power of growth, beginning almost immediately after birth." This same decrease is very realistically shown in the little gastropod, *Litorina littorea*, so abundant on our Atlantic coast. This shell, in the vicinity of Boston, is very quickly attacked by an alga which discolors and erodes it. So if a series of the shells from small to large is collected at mid- or late summer before the new growth has become corroded by the algæ, the amount of that year's growth is very distinctly shown. Such a series shows that, while on the small specimens the year's growth was more than two complete whorls, in older specimens it became progressively less until in some of the mature ones it was but 3.5 mm. Finally on the older shells growth was extremely reduced, being on one shell only 0.75 mm. For these facts concerning Litorina we are indebted to Professor R. T. Jackson whose series of these shells collected from Manchester, Mass., shows the above facts. The series is now on exhibition at the Boston Society of Natural History.

This relative decrease in growth is also shown in the crowding of the septa in old-age cephalopods. Among pelecypods and brachiopods the relative decrease in the amount added to the shell is indicated in the more crowded condition of the later added growth lines. For example, a specimen of *Atrypa reticularis*, No. 641, shows 12 growth lines on the gerontic portion which give a thickness of 5 mm. while the preceding growth, about 22 mm. long, has also only 12. Yet if the growth lines were added at regular time intervals the gerontic stage represented as long a period as that from embryonic through ephebic.

That the more prominent growth lines may define the shell growth for definite periods of time is indicated in the following examples. Buxbaum showed that *Anodonta cellensis*, one of the Unionidæ, had two strongly marked concentric lines and hence three sets of more faintly marked areas, and this shell was known to be three years old (Latter :04, p. 163).

The common oyster commercially marketed is about four years old when gathered. Blue Points, which are smaller, are three years old. This age is broadly indicated on the shells by the stronger growth lines. On the Litorina cited above, the new growth is usually bounded posteriorly by a prominent growth line.

While thus the increase in the size of the animal becomes less and less for each succeeding growth period, a time is reached, varying with each individual, when another factor enters and actual decrease or shrinkage begins. The tendency of the soft parts of animals to contract in old age is familiar to us. (See Hyatt, '96, p. 15; Quain, :03, p. 1478). Through this tendency can be explained many alterations in the hard parts which are otherwise difficult of explanation.

The soft parts and especially the mantle of brachiopods, as well as of molluscs, are so closely related to the shell (Morse, :02,

FIG. 26.— Shell showing gerontic effects produced by injury. *Laqueus californicus* Koch from Catalina Island, California. No. 738, Harvard.

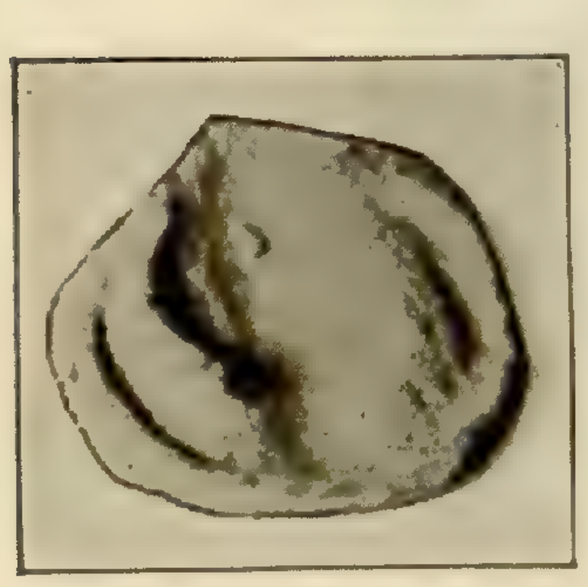
p. 321) that the least change in the former is expressed in the latter. For example, a specimen of *Laqueus californicus* Koch, No. 738, had the anterior portion of the mantle injured. The scars occur in the same relative position on each valve, and the mantle edge left a groove on the shell, indicating the scar (Fig. 26). Before the animal was injured the surface of the shell was very smooth, showing no signs whatever of declining strength, but as soon as the injury occurred a lessened vitality is very noticeable in the change in the angle of curvature and in the lamellose growth lines, simulating senescence.

A change in the angle of curvature of the shell shows that the soft parts of the animal have ceased to grow as fast as formerly. When, however, we consider such gerontic individuals as *Athyris*

spiriferoides, No. 498 (Fig. 6), and *Atrypa spinosa*, No. 499 (Fig. 3), as described above, it is evident that the growth of the soft parts must have practically ceased, while their secreting activities were continued, but were now almost entirely directed toward thickening the shell (see also Beecher, :01, p. 91).

The formation of a groove at the junction of the valves means further, not only that the growth of the mantle has ceased, but that it is in fact growing smaller, in other words is shrinking. As noted above in the description of *Athyris spiriferoides*, etc., the width of the shell on the right and left axis is less during parageron-tism than it is during the earlier anagerontic stage. This tendency of the soft parts of the animal to shrink and to express this shrink-age in the hard parts is also well exhibited among pelecypods and cephalopods.

The lamellosity of the growth lines in such types as Athyris,



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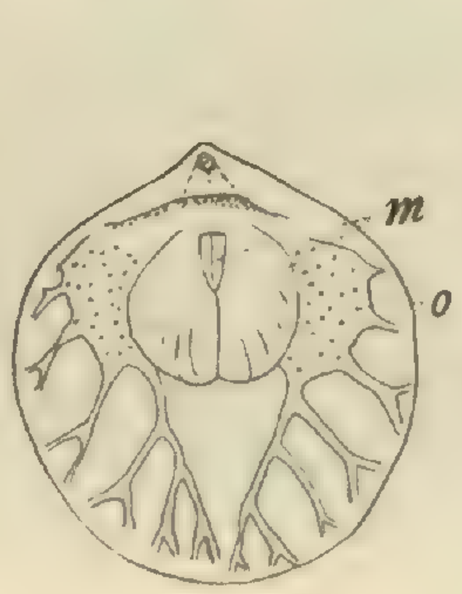

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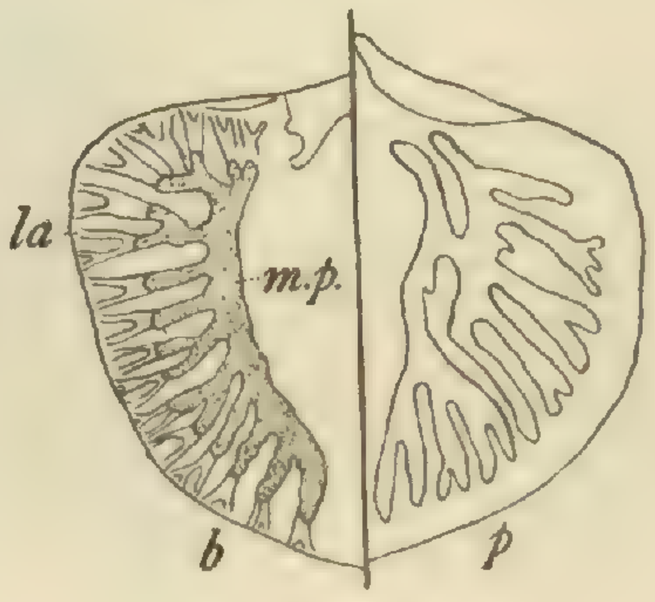

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FIG. 27.— The pedicle valve of a senile individual of *Atrypa reticularis* (Linné) from the Lower Helderberg of Catskill, New York. The prominent ridge surrounding the muscular area occurs beneath the main vascular sinus. No. 641. Harvard.

FIG. 28.— The pedicle valve of *Atrypa reticularis* (Linné) showing the muscular (*m*) and vascular impressions with the ovarian markings (*o*) within the main vascular sinus of the latter. (After Zittel.)

FIG. 29.— Brachial and pedicle half of pallium of the recent *Terebratulina coreanica* with the main pallial sinus and lacunæ filled with eggs. *b*, brachial valve; *p*, pedicle valve; *la*, lacuna; *m. p.*, main pallial sinus (after Morse).

Atrypa, etc., is caused by the relatively decreasing extent of the successive lamellæ of shell growth built in old age. This as resultant brings about a change in the angle of curvature which in extreme cases causes even a resultant angle of less than 90°.

The thickening of the shell on the interior often takes place very irregularly, and leaves the surface strongly papillose. This is well seen in the Spirifers, Stropheodontas, etc. In some Strophe-

odontas, as noted above (section 10), these papillose protuberances become almost spine-like.

The principal thickening in at least many brachiopods occurs over the main trunks of the vascular sinuses (compare Figs. 27, 28, 29; see also Fig. 22). It is a significant fact that in these are located the genitalia (Hancock, '59, p. 817). If a greater contraction took place there it is just in line with what we know occurs in higher animals (Quain, :03, p. 1478). It is usually held that "no gerontic limit is known to the reproductive time in the lower animals" (Hyatt, '97, p. 220). As there is doubtless in most shells an increasing amount of space unoccupied by the soft portion of the animal as it increases in age, it is not necessary to postulate a great shrinkage of the soft tissues to account for the thickening of the shell. Yet the fact remains that in many species the principal thickening is over the main trunks of the vascular sinuses, just where the genitalia occur in modern species and where very probably they were located in fossil ones.

The greater reduction of the lateral growth of the mantle over that of anterior growth in brachiopods is seen in the fact that in old age the shell is proportionally longer than in maturity. The result of these old-age processes appears first at the cardinal angles where the loss of lateral growth to compensate for the shrinkage, causes the flattening-out of the mantle folds (see also Williams, '95, p. 309). The reduction of the radial ribs proceeds progressively from the cardinal angles to the anterior border of the shell and hence it is on the sinus and fold that we find the ribs persisting strongest.

In those cases where the ribs flatten out entirely their continuance is indicated by zigzag lines of growth on the smooth surface of the gerontic portion of the shell. These show that the mantle, after flattening out on one plane, still retained the scalloped border on another. This scalloped edge (as seen for example in *Rhynchotrema capax*) resulted from the faster growing of parts of the mantle over others. As the mantle curved, the parts which formed the summits of the ribs fell behind those which formed the depressions. In other words the portions in the depressions grew faster. This difference in the rate of growth may be seen by following two ribs and their included sinus from the umbo to the front of

the shell, plotting the angles and lengths of the successive growth lines in crossing them (Fig. 30). Thus when the shell surface becomes smooth in old age the zigzag lines of growth where present represent the successive positions of the mantle border. It is as if the plications had been merely transferred from the vertical to the horizontal plane, as the actual mantle is probably scalloped to the same degree in both cases and the absence of ribs results simply from the changed angle of curvature of the shell. Often, however, there is a tendency of the mantle edge to fill out the scallops and to present a smooth edge. A beginning in this direction can be seen at the cardinal angles of many plicate individuals. Examples of this are noted in very old specimens of *Spirifer oweni*, *Rhynchotrema capax*, etc.

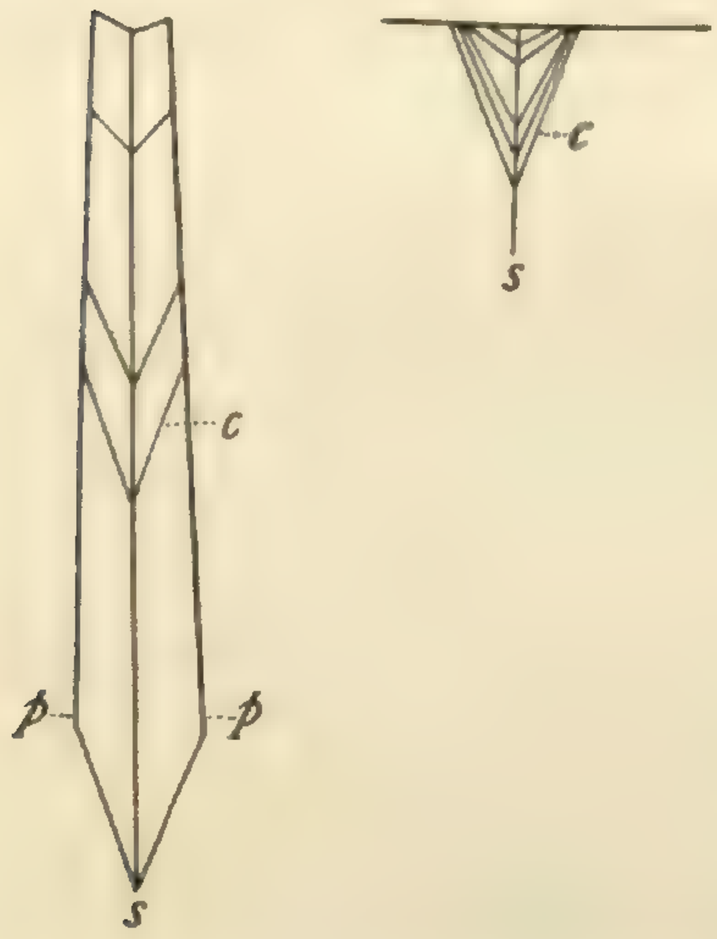

FIG. 30.— Diagrams showing the slower growth of the plications when compared with the furrow between. *a*, enlargement of a furrow and its bounding plications with a few concentric growth lines; *b*, the growth lines of the preceding superimposed on one another, showing graphically the greater growth in the furrow; *p*, plication; *s*, sinus or furrow; *c*, concentric growth lines. These figures were plotted from the median sinus of a specimen of *Rhynchoterma capax*, No. 142, Harvard. × 2½.

The continued anterior growth after the practical cessation of lateral growth causes the cardinal angles to increase in size and causes also the shell index to decrease (see sections 6 and 7). This is a taking-on again of the large cardinal angles and small index of the nepionic stage.

Not only is there repetition of youthful characters in the outline of the shell but there is also a similar repetition in the loss of ornamentation, for the nepionic shell is smooth. An old man with his bald head, curved back, toothless gums, and size smaller than during maturity, resembles the child. Though in these and in many other respects the resemblance is very striking yet in the child the form is the result of positive, developing factors; in the man it is negative, degradational (see also Hyatt, '97, p. 218). So among brachiopods the enlargement of the cardinal angles, reduction of shell index, and the obliteration of ribs, spines, nodes, etc., are in a certain sense a return to the features seen in the nepionic

stage, yet it is a resemblance due to loss of characters. It is thus essentially different from the developing of the similar characters in youth. The characters usually disappear from the shell in the inverse order of their initiation (see also Hyatt, '94, p. 20, and Beecher, :01, p. 269).

As seen above, senility is first shown at the cardinal angles and from there it takes place progressively to the anterior portion of the shell. Hence it is at the cardinal angles that we look for the first expression of old age,— as a change in the angle of curvature, lamellose growth lines, flattening of ribs, and development of a groove at the junction of the valves. Very rarely are individuals found sufficiently old to have expressed on the anterior portion of the shell all of the above senile characters.

When these characters do not appear simultaneously on the shell they appear in a definite order, *viz.*, (1) flattening of ribs, (2) lamellose development of concentric growth lines, (3) change in the angle of curvature, (4) formation of a groove at the junction of the valves, (5) flattening of sinus and fold. This is the usual order, though at the cardinal angles they frequently occur at approximately the same growth line.

Originating thus at the cardinal angles, these gerontic features are pushed farther and farther forward until in parageronticism they are present on the most anterior portion of the shell.

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THE HABITS OF *NECTURUS MACULOSUS*[1]

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NECTURUS although widely distributed throughout eastern and middle North America, is found most abundantly in the rivers tributary to the Great Lakes and in the inland streams and small lakes of the adjoining States. Upon the study of the lake species (*Necturus maculosus* Rafinesque) the following notes are based.

The many names under which Necturus has been described lead to such confusion that some of those most frequently met are here given: *Necturus maculatus, Necturus maculosus, Necturus lateralis, Menobranchus lateralis, Menobranchus tetradactylus, Menobranchus sayi, Menobranchus lacepedii, Menobranchus hyemalis, Phanerobranchus tetradactylus, Phanerobranchus lacepedii, Triton lateralis, Proteus maculatus, Siredon hyemalis, Siren lacertina.* It is known by fishermen and others unacquainted with scientific nomenclature by various names such as: Proteus of the Lakes, Proteus of the Alleghany River, Siren of Barton, mud-puppy, water-dog, water-lizard, fish-lizard, etc.

Size.— According to the writer's observations the adults vary considerably in size, ranging from twelve to eighteen inches. This is based upon an extended series of measurements of individuals taken from different localities and comprising not only the females taken from their nests in the spring, but also both males and females taken in the autumn. It is thus evident that the writer cannot agree with David Starr Jordan ('99, p. 175) and other eminent systematists that Necturus attains a length of 24 inches. In order to ascertain upon what observations these

[1] Rafinesque, in 1818, described this form under the name *Sirena maculosa* (*Amer. Monthly Mag. and Crit. Review*, vol. 4, 1818, p. 41). In 1819, the name *Necturus maculatus* was given (*Journ. de Physique*, vol. 88, 1819, p. 418). In 1820 the specific name *maculosus* was restored (*Annals of Nature or Annual Synopsis of new Genera and Species of Animals, Plants. . . . .discovered in North America. First Annual Number*, 1820. Transylvania University, March 1, 1820. Lexington, Ky.).

statements are based, the literature has been carefully searched.

If we turn to the earliest description, given by Schneider (1799, p. 50) we read: "Corpus ultra 8 pollices longum." This measurement was given for the specimen which he found in Hellwig's cabinet at Braunschweig and which Hellwig had obtained from Lake Champlain. The specimen described by Lacépède ('07, p. 230) was obtained by M. Rodrigues and placed in the Natural History Museum but its original source was unknown. The specimen measured 15 cm.

Mitchell ('21) in 1821 received a specimen from Major Delafield taken from Lake St. Clair. In a descriptive letter written to Professor Configliacchi of Pavia we read the following: "He grows, as I am informed, frequently to the length of two feet. The present specimen is not more than one half that length, one of the smaller having been selected for the greater ease of transportation."

A length of two feet is here mentioned for the first time, and as Harlan ('35, p. 164) has already pointed out, this mistake was due to the fact that Necturus and Cryptobranchus were confused by Mitchell. In a letter written to Charles de Schreiber in 1823 Mitchell ('21) even speaks of Necturus as the creature "which the white fishermen have called by the vulgar name of Hell-bender and the Indians Tweeg." It is not difficult to understand how such an error might have occurred since certain naturalists (Daudin Lacépède, Barton) had considered Necturus as the larval form of Cryptobranchus.

Even Cuvier ('29) writes: "L'espèce la plus connue (Menobranchus) vit dans les lacs de l'America septentrionale, et devient fort grande; atteint dit on, deux et trois pieds." Since this time the error has been repeatedly copied.

Coloration.— The color of the adult is so variable that a description does little more than emphasize this fact; indeed the writer has been so forcibly impressed with this variability that it has led to the surmise that Necturus possesses the ability, more or less common to other Amphibia, of changing its color through its control of the black chromatophores. The animal usually appears a dark ashy brown above, with more or less irregular mottling; below it is more evenly colored and of an ashy flesh

tint. The mottling is due to the presence of large irregular dark areas which are surrounded by a pale yellow margin. Often these spots coalesce to form larger areas or bands. In the younger animals there is frequently a dark band extending from the nostril to the eye, from the eye to the anterior margin of the gills, and from the posterior margin of the gills backward along the side of the body. In some cases the upper surface presents no large areas but is more uniform, and the chromatophores and lipochromes are so distributed that the surface presents a granular appearance. The ventral surface of the body frequently becomes lighter toward the median line and in some a sharply defined linea alba is present. The lower part of the head and tail are frequently dotted with small clusters of lipochromes.

In short, the contrast of black and yellow may in some appear vivid, in others subdued and again disappear almost entirely. It is probable that these variations in color are responsible for a number of specific names. As an instance I might state that some years ago Dr. Garnier ('88) described a small Necturus, taken from the Maitland and Lucknow Rivers in Ontario, to which he gave the name *Menobranchus lateralis*, var. *latastei*. "The colouration above was black, the abdomen sooty and the gular fold white."

During the summer of 1904 the writer was fortunate enough to secure two young animals which measured about 4 and 6 inches respectively. The smaller corresponds closely to the description given by Dr. Garnier and there is every reason for believing that the animal in question is the young of *Necturus maculosus*. The older of the two presents the general coloration of the adult. That Necturus should undergo such striking changes in color may appear remarkable to one who has not studied the early stages but when one has followed the changes in color patterns during growth he finds that they are no less striking and remarkable than in the birds.

Habitat.—The environment to which they are best adapted is not known. In spring and summer excepting the time of egg-laying they are most frequently observed in quiet waters from four to eight feet deep where a clean sandy bottom is fairly well covered by vegetation. In the autumn they are found in pairs

or small groups. From this fact and others to be recorded later it is inferred that this is the mating season.

At times they seem to congregate in large numbers. Milner ('74, p. 62) states that "Mr. George Clark of Ecorse, Mich., had a minnow-seine fitted to the bag of a sweep-net, and at one haul took two thousand of the 'water-lizards.' Estimating the extent that the net had passed over, he calculated the average number of 'lizards,' to each square rod, to be four." Milner again states that "a fisherman at Evanston, Ill., a few years ago had nine hundred hooks set in the lake, and in one day took from these five hundred lizards."

Holbrook says that "they are seldom taken except in the months of April and May." Kneeland states that "they are rarely if ever seen except during the winter." The writer has repeatedly taken them through the ice on set lines during the months of January and February. Reese also reports having taken them through the ice in February. While there are no records showing that they are taken in all the winter months there is but little doubt that they are more or less active throughout the winter, a fact which indicates the absence of a period of hibernation.

Necturus moves from place to place at night and rests quietly beneath boards, logs, or stones during the day. In aquaria they avoid the sunlight, and retire if possible to a shaded portion and always seek concealment. Their movement in the water is slow and is effected by walking, in which act the diagonally opposite legs move in unison. When disturbed they move with celerity through a vigorous lateral motion of the broad and powerful tail, with the feet closely applied to the body and motionless. They never swim long distances, at most a few yards, then seek concealment either in the mud or beneath some object.

One is rarely fortunate enough to get a glimpse of them during the day; they seem to be extremely sensitive and disappear at the slightest disturbance of the water, such as that caused by the approach of a boat. If they are undisturbed, one usually sees the head protruding from beneath the concealing object. The animal thus presents a curious appearance with its ruby gills moving gracefully to and fro. When they are disturbed the gills change from their bright red to a dusky color and are at once drawn down tightly against the neck.

When these animals are retained in aquaria they are frequently observed to thrust their snouts above the water, open the mouth widely, and then return to the bottom where they soon expel the air both through the gill slits and from the mouth. It would thus seem that while the branchiæ are the chief means of respiration the lungs play considerable part. Kneeland ('59) made some very interesting observations on this point which are here quoted. "He put two of these reptiles into an aquarium with half a dozen minnows, varying in size from two to three inches. The fish were frequently seen nibbling at the expanded gills of the reptiles, which as often suddenly darted from their ordinary state of repose, attempting to seize the fish, which they never succeeded in doing. In about ten days the menobranchs had nothing left of the gills but the almost bare cartilaginous supports, with only here and there a branchial fringe. The fish were then taken out, and the branchial fringes began to grow again, and in the course of six months had regained about half their normal size. He had watched these reptiles for two summers, and no similar falling of the gills ever took place, so that it appears in the present instance that the fish actually eat them off, their loss being a pathological and not a natural phenomenon. In either case this fact seems interesting from a physiological point of view, as bearing upon the respiratory organs of these reptiles. He had ascertained experimentally that they survive out of water about four hours, showing that their pulmonary sacs, or lungs, are not alone sufficient for the maintenance of respiration. In the present instance, though their pulmonary sacs were the principal respiratory organs, the animals did not apparently suffer. . . .

"The question arises, why are these lungs apparently sufficient for respiration in the water and not in the air, though the respired element be in both cases the same? As there is no evidence of internal gills, the reason must be that in the air the branchial tufts from dryness are unfit for circulating the blood, the complimentary respiration of the skin, so important in reptiles, cannot be carried on — the pulmonary sacs alone are insufficient for the aëration of the blood, and the animal dies. In the water, however, even though the branchiæ, as in this case be useless, the cutaneous respiration is unimpeded and with the pulmonary

is sufficient for the purification of the blood. This fact shows the importance of the cutaneous respiration and the insufficiency of the pulmonary."

Food.— Concerning their natural food little is known beyond the fact that dissections of the alimentary tract reveal the presence of small crustaceans, insect larvæ, and occasionally a small fish. Harlan ('35) and James ('23) both record having found earthworms in the alimentary tract. Kneeland ('58) says: "They seize living worms eagerly and suck them down, if small, with a single sudden swallow; if the worm be large, it is swallowed by repeated suctions, the teeth preventing its escape; the act of suction may be seen by the movements of the impurities in the water, as it is drawn in and afterwards expelled. They often miss the worm; sometimes it may be too far off, but at others so close to them that it seems that their vision must be imperfect. They will not eat a dead worm unless they have been kept without food for a considerable time."

A very curious performance was witnessed by Kneeland and reported by the secretary of the Boston Society of Natural History as follows: "A number of Necturi had been without food for five months when four living minnows were placed in the aquarium, three of the four minnows were swallowed before the expiration of fifteen minutes, and among them the largest. After they had swallowed them, they seemed very uneasy, moving the bones of the head and jaws, and contorting their bodies in various ways, as if they did not feel quite easy in their stomachs; however they at last became quiet, but at the end of twenty hours they became uncommonly active, and the three fish were regurgitated with the scales off, the eyes out, and the entrails of the smallest gone; they were perfectly white, and looked like ghosts of fish. It was either diet to gross for their delicate and weakened stomachs, or else not sufficiently comminuted for the action of their gastric juice." Garnier says that they eat small living fish and crayfish by preference, and do not readily take meat in captivity.

Montgomery states that "from observations of the Menobranchus in an aquarium plentifully stocked with molluscs, such as Physidæ, Limnæans, Paludinæ, Planorbes, Anodonts, etc., as

well as crustaceans I am not warranted in asserting that it feeds on anything other than true fishes."

Milner quotes Clark as stating that "those taken at Ecorse, Mich., were so gorged with white-fish spawn that when they were thrown on shore, hundreds of eggs would fly out of their mouths."

The writer has tried to feed them with various kinds of food. Necturus will readily eat living earthworms but will pay no attention to dead ones. Pieces of liver which are held in forceps and moved gently through the water in close proximity to the snout they seize and devour. But the most satisfactory food is small minnows which at intervals are placed in the aquaria. The movements of the minnows seem to excite the animals whose heads are soon seen protruding from beneath the concealing objects. When the minnow comes in close proximity there is a flash-like movement toward the minnow which in turn either escapes or is swallowed. The writer has observed repeated failures to catch the minnow, but the persistence of the animal is remarkable and it sooner or later succeeds.

From the fact that whenever the water is disturbed in the vicinity of the snout they snap viciously one is led to infer that in taking food they rely almost entirely upon the tactile sense.

Necturus is much dreaded by the ordinary fishermen who regard them as poisonous as do also the Indians (Durkee). According to Gibbes ('53) the negroes are terrified by its presence. He says that "the piggin or wooden vessel, in which an animal was placed after its capture, was destroyed by the negro to whom it belonged, who was resolved never to carry food in it or eat out of it again." Notwithstanding this popular superstition the animal is perfectly harmless and may be handled at pleasure. Its flesh is white and said to be very palatable by Wilder ('74) who writes as follows: "In preparing a paper upon their anatomy and embryology, Dr. W. S. Barnard and myself have had occasion to use them in numbers; and a single fisherman, who sets many hooks for fish has brought us a hundred during the past month (March); he, and all others, apparently regard them as poisonous, and are rather averse to touching them; so far is this from the case, that they are absolutely harmless in every way: and on the 5th Dr. Barnard and myself ate one which was cooked,

and found it excellent: it is our intention to recommend it as food, but not until our investigations are complete."

Their great tenacity of life is a matter of frequent comment. They seem to be able to live for months without food. They have been left for three or four hours out of water and are then easily revived. After severe mutilations they recover, but notwithstanding this great vitality they seem to fall easy victims of a fungus which has not as yet been determined specifically. Mr. Browne (Milner, '74) of Grand Haven, Michigan, states that "some years ago, an epidemic seemed to prevail among the Menobranchi in Grand River, in the month of June, and that their carcasses were washed ashore by hundreds, so that they lined the banks of the river and the mill-men were obliged to throw the bodies off into the current, to be carried down stream to prevent the offensive stench that was wafted into the mills from the decaying remains."

Casting of Epidermis.— Kneeland ('57) states that Necturus sheds its epidermis in the winter. "They shed their skins at this season; I have had several with the old skin hanging to the new in shreds and patches, which are washed off by the water in two or three days, leaving the colors of the new skin very bright; the edges of the tail are then so thin and transparent that the network of blood vessels can be seen with the naked eye."

While endeavoring to obtain a photograph of Necturus on February 9, 1897, Mr. A. H. Cole, one of my students, observed the animal cast its epidermis. His notes read as follows: "The epidermis as a thin layer appeared to have loosened from the entire surface of the body, appearing frosty-white with bubbles of air. The loosened epidermis was split along the mid-dorsal line, its free edges floating upward in ragged streamers. On the following day none of the epidermis remained excepting glove-like portions which were yet attached to the feet; these portions were not cast until two days later."

Breeding Habits.— Although more than a century has elapsed since Necturus became an object of special study on the part of both American and European naturalists, no one seemed fortunate enough to obtain embryological material until Professor

Charles O. Whitman some eighteen years ago discovered the nests and obtained a complete series of developmental stages.

Those who sought the embryological material were forced to enter an unexplored field. No one felt certain that he had even found the adult animal, since the error of Mitchell, that the adult measured two feet, had been and is yet, copied by the leading systematists. Moreover, Barton (Gray, '57, p. 61) held that the animal was the larval form of Cryptobranchus. Cope ('66) expressed the opinion that it was a larval Sperlerpes and changed in the same manner as the Siredon to an Amblystoma. Baird ('50) suggested that it might be the unmetamorphosed form of some great salamander as yet unknown. If the above were true it then remained to be determined whether the animal bred in the larval or the adult condition, or in both. All these possibilities demanded careful consideration.

Again it was not known whether they were purely aquatic or whether they came frequently on land, as described by Smith ('32), DeKay ('42), and others. When this question was answered others arose, and foremost among these was the time of breeding. Concerning this period there were numerous conjectures. Kneeland ('57) states that the animals were taken in abundance near the shore during the winter months. "The reason why they approach the shore at this season may be on account of this change in skin, and possibly for breeding purposes. About once a week they pass from the anus a gelatinous mass, about the size of a pea, of a whitish color, I thought this might be possibly an egg, but the envelope soon becomes soft in water, and its contents are lengthened out into a somewhat convoluted form."

Holbrook ('42) observes that they are "seldom taken except in the months of April and May which is their spawning season. Their eggs are about the size of peas and as many as one hundred and fifty have been counted in a single female."

Milner ('74) states that a "full series was this season ('73) collected from the Detroit River, from the length of one and one fourth inches to thirteen inches. Later, about the middle of the month of July, Mr. George Clark collected a quantity of their eggs, proving this month to be the spawning season of the animal."

Spring, summer, and winter were each regarded as the breeding season and, so far as the observations were concerned, with equal degrees of probability.

Thus there was little to be gathered from the observations previously made. The only reliable data were to be obtained through a systematic examination of the ovarian eggs at different seasons of the year. Even when this tedious work had been carried out and clews obtained as to the egg-laying period, other and greater difficulties arose. The Great Lakes and their tributary streams in which Necturus had been reported most abundant were usually so clouded by muddy water that search for eggs was futile. Localities must be found where the animals were plentiful and where the water remained clear. The small inland lakes of eastern Wisconsin seemed best to fulfil these conditions. Again, no one knew or had even suggested where the animals deposited their eggs, whether in deep or shallow water, whether they were laid in masses in open places like those of Amblystoma, or scattered in strings like those of the toad, or laid singly and concealed among the leaves and branches of aquatic plants like those of the newt.

The knowledge of the egg-laying habits of other Amphibia gave no clue, but nevertheless the work was continued and after years of persistent and patient effort Professor Whitman finally discovered the nests and eggs of Necturus. Only those who have for years been baffled in their attempts to obtain the embryological material of other North American Urodeles, such as the Siren, Amphiuma, and Cryptobranchus can properly appreciate the enormity of the task.

Through the kindness of Professor Whitman the writer first obtained a knowledge of the habits and breeding places of Necturus, and each summer for the past eight years has made observations on the habits of these animals in their natural environment.

Egg-laying.—The time of egg-laying varies in different lakes, depending upon the time when the temperature of the water reaches a certain degree. In the larger, deeper lakes with bold shores this is much later than in those possessing wide shoals. Again, in the individual lakes the time is dependent upon the same conditions. The eggs are first deposited in those localities where the water is shallow and exposed for the greater part of the day

to the sun. The period of egg-laying usually covers two or three weeks. There is no foundation whatever for the statement made by Hans Virchow[1] that the animals deposit their eggs so to speak at the same hour.

According to Professor Whitman's and my own experience the best time for collecting is during the middle and latter parts of the month of May. The writer has collected eggs as early as May 3, and as late as June 5, but these extremes mark the beginning and closing of the early and late seasons.

Preparatory to egg-laying, Necturus seeks the sandy shoals of the lakes or streams. They seem to prefer those localities where the bottom is strewn with numerous logs and boards. It is more than probable that the animals seek these grounds at night since they are rarely if ever seen moving about during the day.

During the day they lie quietly concealed beneath the various objects and one not familiar with their habits would rarely if ever detect their presence. If one desires to see the animals in their natural positions he must approach with much care and he may perchance be rewarded by seeing the head of one protruding. If, however, the jar of the boat or the scraping of an oar has caused them to hide, he must overturn the concealing object. If this is done with great care the animal is occasionally undisturbed and lies for some time motionless, then begins to crawl slowly about. If, however, the disturbance be violent it darts away and conceals itself beneath some other object.

The nest of Necturus, if indeed, such it may be called, is, as has been said, always carefully concealed beneath some object and consists of nothing more than a slight excavation in the sand with a narrow opening through which the animal's head protrudes; the nest is thus perfectly guarded against the attacks of enemies. The objects beneath which the nests are most frequently found are clean logs or boards which lie partially imbedded in

[1] *Sitzb. Ges. naturf. Freunde zu Berlin*, 1894, p. 37: "Necturus kommt in den zalreichen Seeen im südlichen Wisconsin häufig vor und auch an anderen Stellen der Vereinigten Staaten. Die Laichzeit ist nach mündlichen Angaben der Brüder Meyer Mitte Mai, im Jahre 1893 fiel sie auf den 22. Mai, d. h. später wie gewöhnlich; sie variirt nach dem Wasserstande. Die Thiere legen nicht zu verschiedenen Zeiten ab, sondern angeblich zu g[eicher Zeit, sozusagen auf dieselbe Stunde."

the sand. The writer has also found them beneath pieces of tin, canvas, and even an old hat.

The depth of the water in which these nests are found, is variable. The writer has found nests covered by only four inches of water, again a nest was found beneath a board at a depth of ten feet, but these are unusual conditions. The majority of nests are found at a depth of from two to four feet. The nests are often found in close proximity to one another; and it is not at all exceptional to find several nests on a single board frequently not more than a foot or two apart. In one instance ten nests were taken from a single board not more than twelve feet long.

In order to facilitate the collection of eggs it has been found advantageous to place boards in suitable localities during the early spring months. When the breeding time has come many of these shelters will have been chosen as nesting places.

During egg-laying the males are never found with the females, and where they remain is unknown. In just what manner the female deposits the eggs is also problematic. There are different stories told by those who during recent years have acquired some knowledge of their habits. In some way the female brings her body in such a position that the eggs are deposited on the sheltering object. When the laying is finished the eggs are found scattered over a surface from six to twelve inches in diameter. The eggs are attached singly by the outermost of the three enclosing envelopes and are about a quarter of an inch in diameter, of a pale cream-color, sometimes showing a faint tinge of green.

The period of deposition undoubtedly covers many hours and probably in some instances, days, since in several cases all the eggs were removed from nests and the following day freshly deposited eggs were found. Further proof is found in that the same nests frequently contain eggs in both early and late cleavage stages. This supposition is further confirmed by the fact that some days after the beginning of egg-laying the oviducts yet contain mature eggs.

If one wishes to leave the nest in such a condition that the female will return and continue laying he must exercise great care in replacing the object to which the eggs are attached. If the nest be much disturbed, one will find upon his return for a fresh

supply of eggs, that even those which were left are missing. Several times the writer has found an animal in the nest whose stomach was distended with eggs. The inference, although positive proof is wanting, is that the parent devours her eggs when the nest is much disturbed.

The length of time which intervenes between deposition and the beginning of cleavage has been accurately determined in a single instance in which four eggs were deposited after the animal was placed in the aquarium. These were placed in a hatching dish in which the water was 17° C. In one egg the first cleavage groove appeared in 18 hours, in two at 20 hours, and in one at 23 hours. The time in some cases certainly exceeds 24 hours, since eggs taken from the nest were kept in a hatching dish for this length of time before cleavage began.

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NOTES AND LITERATURE.

ZOÖLOGY.

Kellogg's American Insects.[1]— It is gratifying to observe the great progress that is being made in the science of entomology, and to welcome a book such as the author now brings before the public. While the biological side is strongly emphasized it is not overdone and we have the subject presented in a much broader sense than has perhaps ever been done in a single volume. It is written in a clear and popular style, and the fact that the species of economic importance are more fully treated adds much towards making the work of general interest. The 674 pages are illustrated by over 800 figures in the text and 18 colored plates, well selected to show the biologic, systematic, and economic features in the study of insect life.

The first chapter treats of the structure and special physiology of insects, and the second of the development and metamorphosis, followed by the classification and description of the various groups arranged under 19 orders, with keys to the families and many of the genera.

The student will naturally compare this work with that concise and well balanced volume, Comstock's *Manual*,— a work dearer to the hearts of American entomologists to-day than a year or two after its publication. While the new work is quite different in its general makeup, and of a more popular nature, it has not been edited with as much care, but, considering the size of the volume there are comparatively few mistakes, and those which might be misleading to the young student can be briefly noted as follows: on page 201 the figure of *Ranatra fusca* represents either an imperfect specimen, without wings, or an immature example; the respiratory tube is also poorly shown; Fig. 317 is a Micromus not Hemerobius; *Coptocycla aurichalcea*, Fig. 389, and *Cassida bicolor* mentioned in the text (page 281) are synonymous (the latter specific name is now used); Fig.

[1] Kellogg, Vernon L. *American Insects*. New York, Henry Holt and Co., 1905. 8vo, vii + 674 pp., 13 pls., 812 text figs. $5.00.

463 is *Dasyllis sacrator*; Fig. 500 is *Sepedon fuscipennis* not *fasci-pennis*; Plate 12, Fig. 3, is *Synchloë reakirtii* not *genutia*; Plate 13, Fig. 3 is an *Elis* sp.; Figs. 681 and 682 undoubtedly represent the same species. Although questioned, it is hard to account for Fig. 684, which belongs to an entirely different family; the male of *Pelecinus polyturator* is figured in Packard's *Guide to the Study of Insects*.

Following the chapters devoted to the descriptions of the various orders is a very interesting chapter on insects and flowers in which the pollination of various plants by insects is described. A chapter on "Color and Pattern and their Uses" presents a subject open to much criticism. There is a tendency to carry the so called "mimicry," or preferably protective resemblance, beyond the limits of our every-day walks in the fields and woods, *i. e.*, to emphasize this feature by selecting the most pronounced forms from the fauna of the world and arranging them in museums regardless of their natural surroundings. The "dead-leaf butterfly" (Kallima) is very effective arranged on a twig among the dried leaves of the elm or beech, but when we read that the butterfly usually alights on the trunk of the tree head downward, the charm is broken. Our various species of Polygonia (Grapta) and several groups of moths present fully as interesting examples of protective resemblance. A very instructive and timely chapter is devoted to insects and disease. The work concludes with an appendix on collecting and rearing insects.

C. W. J.

Kingsley's Elements of Comparative Zoölogy.[1]— In this second edition of Kingsley's *Elements of Comparative Zoölogy* the most marked changes from the first edition (1897) are due to a rearrangement, the descriptive part being separated from the laboratory directions and brought together to form the last two thirds of the book, under the heading, in the table of contents, of "Systematic Zoölogy." This plan, which is that adopted by the same author in his *Comparative Zoölogy of Vertebrates*, would seem to be of distinct pedagogical value owing to the confusion in the student's mind arising from the discontinuity of the other arrangement. The questions for a tabular comparison of the forms studied and the groups to which they belong — an especially valuable feature — have been retained, and in a few cases somewhat extended. On page 108 there is a repetition of questions (3 and 7) which should be corrected.

L. J. C.

[1]Kingsley, J. S. *Elements of Comparative Zoölogy*. Second edition, revised. New York, Henry Holt and Co., 1904. 8vo, x + 437 pp.

Punnett's Mendelism.[1]— A useful popular exposition of Mendel's law of heredity. It contains a brief biographical sketch of Gregor Mendel, an account of his experiments in hybridizing plants, the rediscovery of his law of heredity long after Mendel's death, with numerous examples of Mendelian inheritance in animals as well as in plants. No complete account is given of the development of Mendelian theory since 1900, nor does the book contain a bibliography.

W. E. C.

Hantzsch's Birds of Iceland.[2]— This substantial contribution to faunal ornithology is a good example of the present-day "local list," or *résumé* of the avifauna of a circumscribed area. Iceland, because of its position and physical features, affords an unusually interesting field for study. The grass-lands, the moors, the barren mountain tops, the glaciers, rivers, woods, and sea here provide a variety of country, but the rigorous environment is unsuited to many land birds.

The author in his introduction, summarizes briefly the ornithological literature of Iceland, and at the end of the chapter lists the more important works dealing with Icelandic birds. The topography of the island is then treated and the species peculiar to the different areas are listed. An interesting feature is the hot springs which never freeze in the winter and make it possible for certain species to pass the cold season in their vicinity far to the north of their usual winter range.

A number of changes in the avifauna within historic times are noted. Certain birds of prey have evidently decreased, as have also certain fresh-water ducks. Eider ducks, owing to recent protective legislation are more abundant now than formerly. The cliff-breeding Alcidæ are for the most part holding their own. The Great Auk was exterminated in Iceland in 1844. Following chapters deal with the derivation of the birds of the region, their migrations, and their economic importance to the Icelandic people. The migrations are of particular interest and might well have been treated in more detail. A number of wanderers reach Iceland during the fall migrations,

[1]Punnett, R. C. *Mendelism*. Macmillan and Co., London, 1905. 16mo, vii + 63 pp.

[2]Hantzsch, Bernhard. *Beitrag zur Kenntnis der Vogelwelt Islands*. Berlin, R. Friedländer and Sohn, 1905. 8vo, vi + 341 pp., 26 figs., 1 map. 12 Marks.

having evidently been blown out to sea by southerly storms in crossing from Norway to the lands to the south. Migrants to the far north and Greenland pass through on their migrations, or come down in fall to winter, for the warm Gulf Stream waters keep the southern coast of Iceland largely open in the cold months. The fall migration of native birds is chiefly to the southeast, *via* the Faröe Islands to the British Isles or to southern Norway, and the reverse in spring.

The second part of the book is devoted to the annotated list of Icelandic birds, with synonymy, and notes on the habits. One hundred and twenty species are recorded as certainly known, exclusive of the Great Auk. The greater part of these are water birds, and some thirty-two only are land birds, of which latter, but twelve are known to breed in Iceland. In the notes relative to the different species is brought together a great mass of valuable information largely the result of the author's personal experience. A few of the more interesting notes are the account of the nesting of *Megalestris skua*; the occurrence of a single specimen of the Yellow-nosed Albatros (*Thalassogeron chlororhynchus*) for several seasons on the south coast until shot (in 1846); the nesting habits of Barrow's Golden-eye Duck; and the occurrence of such American species as the American Widgeon, Belted Kingfisher, the Lapland Longspur (rarely noted with flocks of Snow Buntings).

The author's use of Latin names differs somewhat from the accepted usage of American ornithologists. Thus the Kittiwake is *Rissa rissa;* Palidna is used as an emendation of Pelidna. We are glad to note, however, that the Ringed Murre is not considered a distinct species from *Uria troile.*

G. M. A.

Holder's Half Hours with the Lower Animals.[1]— Dr. Holder, to use his own rather awkward phraseology, has "endeavored to make this volume a popular combined review and supplemental reader on the lower forms of animal life from the Amœba to the insects inclusive." There are twenty-nine chapters, twelve of which are devoted to the different families of insects, four to crustaceans, and one each to most of the other groups. It seems to the present reviewer a mistake to have attempted the combination of text-book and reader. The result is neither fish, flesh, nor fowl. There is

[1] Holder, Charles F. *Half Hours with the Lower Animals. Protozoans, Sponges, Corals, Shells, Insects and Crustaceans.* New York, American Book Company, 1905. 8vo, 236 pp., illus.

a great deal of information about the more interesting species, enlivened by bits of personal observation on the Florida reefs and off the California coast. Every now and then the author remembers that the book was also intended for a text-book, and injects accounts of the external or internal anatomy of the group or species under discussion with references to accompanying figures. There is constant evidence either of careless throwing together of notes or of a very poor literary handling of material. On page 81 the reader has been hearing about Lingula for nearly two pages, when suddenly in the very midst of a paragraph he takes a flying leap into a Sikh rebellion in India and is put to flight by a horde of land leeches which drop from the trees. On page 213, the author, speaking of butterflies, refers to a figure of the head of a moth; moreover the figure shows the pollinia of an orchid attached to the moth's eyes, and the reader is allowed to assume that they are a structural part of the head.

The book has decided merit as a reference book or a supplementary reader for a class in nature study. If the author had not coquetted with the text-book idea, and had arranged his material with more care, the book could have been greatly improved. The illustrations are excellent.

R. H.

Notes.—*Additional Records for New England Crustacea.* Since the publication of Miss Rathbun's list of the New England Crustacea (*Occasional Papers Boston Soc. Nat. Hist.*, vol. 7, no. 5, July, 1905) the writer has gone over the study series of the Society's collection and the more recent acquisitions. During this work notes were made when the specimens found added something to the records published in that list, either in the way of localities, extension of range, or the animals with which the crustacean was associated either as a parasite or in a symbiotic relation. These records follow:—

Uca minax (LeConte).— Above Fall River, on the Taunton River, were found all three species of Uca; on sandy flats on the outer river bank were found *U. pugnax* (Smith) common, and *U. pugilator* (Bosc.) a few. In Thatch Pond, a somewhat protected area, were found *U. pugnax*, a few, and *U. minax* (LeConte) very plentifully.

Sesarma reticulatum (Say).— A single specimen of a male from Bristol, R. I., and several specimens from Wood's Hole, Mass.

Pinnotheres maculatus Say.— Specimens from gills of *Modiolus modiolus* Linné, Vineyard Sound.

Pagurus pollicaris Say.— A single specimen from Beverly Bridge, Mass., collected by J. H. Emerton, gives a northward extension to the range of this species.

Cirolana polita (Stimpson).— Specimens from Ipswich, Mass.

Ægа psora (Linné).— Single specimens from Head Harbor, Me., Matinicus Island, Me., and off Thatcher's Island, Mass.

Nerocila munda Harger.— Specimens from fins of file fish; Buzzards Bay, Mass.

Chiridotea cœca (Say).— Eastport, Me.

Asellus communis Say.— Salem (J. S. Kingsley, coll.) and Boston, Mass. (S. Henshaw, coll.).

Tryphosa pinguis (Bœck).— Eastport, Me., (A. S. Packard, coll.).

Ampelisca macrocephala Lilljeborg.— Specimens from Grand Manan give a more northern record. There are also specimens from No Man's Land, Mass. (A. Hyatt, coll.).

Ampelisca compressa Holmes.— Also from No Man's Land, Mass.

Byblis gaimardii (Kröyer).— Eastport, Me.

Haploöps robusta G. O. Sars.— Massachusetts (H. B. Storer, coll.).

Acanthazone cuspidata (Lepechin).— Eastport, Me., and off Cape Ann, Mass., 25 fathoms.

Lafystius sturionis Kröyer.— Cape Ann, Mass., on cod.

Pontogeneia inermis (Kröyer).— Eastport, Me.

Dexamine thea Bœck.— Beverly Harbor, Mass., (J. H. Emerton, coll.).

Gammarus annulatus Smith.— Noank, Conn.

Mæra danæ (Stimpson).— Eastport, Me., and off Cape Ann, Mass.

Ischyrocercus anguipes Kröyer.— Eastport, Me., and Marblehead Neck, Mass., (J. H. Emerton coll.).

Ericthonius rubricornis (Stimpson).— Eastport, Me., and off Cape Ann, Mass.

Dulichia porrecta (Bate).— Eastport, Me.

Ægina longicornis spinossima Stimpson.— Salem, Mass.

Caprella linearis (Linné).— Annisquam, Mass.

Lepas anserifera Linné.— Portland, Me., from vessel.

Lepas fascicularis Ellis and Solander.— Eastport and Pemaquid, Me., Ipswich Bay and Lynn, Mass.

Lernæa branchialis Linné.— Annisquam, Mass.

Eubranchipus vernalis (Verrill).— Cohasset, Mass.

Joseph A. Cushman.

BOTANY.

Smith's Bacteria in Relation to Plant Diseases.[1]— Bacteriologists have long awaited Dr. Smith's work on the bacterial diseases of plants. We are now favored with the first part dealing with the methods of work and general literature of the subject. The monograph is not intended to take the place of the many text-books on the subject, but rather to supplement them. The work will be found useful to animal pathologists, as well as to plant pathologists. The monograph is the outgrowth of the work which has been carried on in the study of bacterial diseases of plants in the Laboratory of Plant Pathology, United States Department of Agriculture. The methods described have all been tested and are now in use in the Department. The following suggestions in regard to "A Study of an Organism" should be impressed on every beginner.

"Every one who has carefully inquired into the matter knows that the brief statement of the behaviour of an organism on nutrient agar, on gelatin, and on two or three other media, with perhaps a loose statement of its color and size, no longer constitutes a description which describes. Such accounts, of which there are a great many, usually fail to mention just those things which might serve to distinguish the organism from its fellows. If a new species is not to be described so that it can be identified by others, what then is the use of any name or description? The name will only serve to encumber future synonymy and to recall the incapacity of its author." The following opics indicate the broad and comprehensive scope of the subject matter: The Disease, The Organism, Physiology, Relation to Free Oxygen, Luminosity, Bibliography, General Literature, and Formulæ.

The author states that great stress should be laid on the minute morphology in a variety of cultures. He recommends especially the use of photography in microscopic work, which Dr. Koch has said "would certainly have prevented a great number of unripe pub-

[1] Smith, Erwin F. *Bacteria in Relation to Plant Diseases — Volume* 1, *Methods of Work and General Literature of Bacteriology exclusive of Plant Diseases*. Publication No. 27 Carnegie Institution of Washington, 285 pp., 31 pls., 146 text figs.

lications." Not only is it necessary to determine motility, but the organs of motility should be stained. The part of the work dealing with culture media is an excellent treatise; every working bacteriologist can get many valuable suggestions from it. The many conflicting statements as to the behavior of organisms by different authors arise largely from the character of the media used. In regard to vegetable media, he prefers to have them sterilized in the steamer rather than the autoclave. If boiling changes the nature of any fluids it is advisable to use the Chamberland or Berkefeld filter, but Chamberland bougies should not be used continuously for more than three days, because of the growth of small organisms in the walls of the filter, when they should be sterilized. There is a highly interesting discussion of sensitiveness to plant acids. The *Bacillus tracheiphilus* is used to show tolerance for sodium hydrate. Its tolerance for this substance can be considerably increased by inoculating each time from alkaline bouillons rather than from acid ones. The thermal relations of bacteria are among the most interesting and should be studied with great care. Under the head of economic aspects of the subject he argues with force that more attention should be given to the collection of accurate statistics by competent persons as an aid to legislature and governments. There are some excellent suggestions on natural methods of infection, how the parasites are introduced from one field to another by the roots of plants and in plants. The soil is a living thing and should not be transported from one field to another carelessly; the parasite may gain an entrance through wounds, by way of the stomata, lenticels, water pores, and nectaries. The keeping of records is an important part of the work of the experimenter, and it would be well for every bacteriologist to have Dr. Smith's work at hand and follow carefully the outlines given. The beginner should also be interested in the card-catalogue system used by the author.

The systematist will be interested in his discussion of nomenclature and classification, a subject naturally in a very chaotic state because systematic botanists have given so little attention to it, and medical men have cared even less about the classification of bacteria. He does not think it advisable to use Bacillus 1, 2, or 3 or A. B. C.; if the organism is really new and distinct, it should be given a name. Every working botanist will agree with him that all polynomials like *Bacillus coli-communis* are to be regarded as "*nomina excludenda*." We agree also that all species antedating the Koch poured-plate method, which are not accurately described, should be abandoned.

"The *Micrococcus pellucidus*, although published quite recently and in the *Comptes Rendus* of the French Academy, is not described any better." "I find it quite impossible," says Mr. Stoddert, "to identify many species from published descriptions." Numerous complaints of this sort, made in recent years by well trained and competent men, sufficiently indicate the necessity of a thoroughgoing reform. He makes a plea for better and more careful descriptions, and concerning the use of the uncertain old names says: "And here I wish to register a protest against anything of this nature ever being done. If, in his own generation, a name cannot be associated beyond doubt with a particular organism by means of an author's description or figures or collected specimens, then this name should disappear, never to be revived. Societies of bacteriologists should unite in the near future on some authoritative date for the beginning of species priority, so that some sort of stability may be guaranteed to the nomenclature of the future."

In this part of the work there is a good discussion of the more modern systems of classification, that of Dr. Alfred Fischer, 1895, and the Migula classification, the latter of which is largely followed in this country. He then gives descriptions of the following orders and families: order Eubacteria, family Coccaceæ (Zopf emend.), Mig., family Bacteriaceæ, family Chlamydobacteriaceæ; order Thiobacteria, family Beggiatoaceæ, family Rhodobacteriaceæ, subfamily Thiocapsaceæ, subfamily Lamprocystaceæ, subfamily Thiopediaceæ, subfamily Amœbobacteriaceæ, subfamily Chromatiaceæ, to which he has very properly added the Myxobacteriaceæ. Some changes are proposed in nomenclature of genera and species. The genus Bacterium (Cohn) takes the place of Pseudomonas of Migula. The *Pseudomonas campestris* becomes *Bacterium campestris*. The *Bacillus anthracis* of Cohn is the type of a new genus, Aphlanobacter. The organism then should be called *Aphlanobacter anthracis* (Cohn) E. F. Smith. The genus Vibrio (Muller, Cohn) includes the *Spirillum cholera-asiaticæ*. Otherwise he follows the classification of Migula. There are good grounds for the changes here proposed.

The author has brought together formulæ for stains, synthetic and nonsynthetic culture media, tests for indol, and fixing fluids. Sixty-three pages are devoted to bibliography, well arranged and frequently provided with abstracts of the papers. Many excellent plates accompany the paper. The frontispiece contains halftones of five eminent bacteriologists: Ferdinand Cohn, Robert Koch, Louis Pasteur, Emile Roux, and Emile Duclaux.

This volume is the most important piece of general bacteriological literature that has been published in this country. It would be well indeed to have a copy of it in every working laboratory.

L. H. PENNUEL

A Bibliographical Index of North American Fungi.[1]— For about thirty years Professor Farlow has been accumulating a card index referring to the fungi of North America. Nearly twenty years since, two authors' lists of works on this subject were published, and have been kept at the elbow of every student of our fungi since their appearance. The publication has now been commenced of the references to genera and species, as Publication No. 8 of the Carnegie Institution.

The preparation of an index may appear to the uninitiated a simple matter. A perusal of the author's seven-page preface is calculated to undeceive one who holds such an opinion, and the preface also contains some of the most sensible of recent commentary on nomenclature in natural history. A full list of abbreviations, and their consistent use, have rendered possible a wonderfully condensed presentation of the references to publications, which are kept within the limits of a single text line each. Synonyms are intelligibly collocated with accepted names, and free use is made of cross references.

In the preparation of the index, the author has had the assistance of Mr. Seymour's keen eyes for many years, and it may be predicted with safety that no important omissions will be found. Dr. Farlow's own familiarity with the literature of his subject is second to that of no one, and the knowledge of fungi that he has brought to the acceptance of admitted names, the placing of those treated as synonyms, and a very free critical annotation, is unequalled.

The Carnegie Institution is to be congratulated on having undertaken the publication of so generally useful a work as the *Index of North American Fungi*, the value of which in facilitating thoroughness of study is certain to make itself felt in all future publications on this important subject.

W. T.

Osterhout's Experiments with Plants.[2]—This book brings before

[1]Farlow, W. G. *Bibliographical Index of North American Fungi. Vol.* 1, *part* 1, "*Abrothallus*" *to* "*Badhamia.*" The Carnegie Institution, Washington, Sept. 1, 1905. 8vo, xxxv + 312 pp.

[2]Osterhout, W. J. V. *Experiments with Plants.* New York, The Macmillan Company, 1905. 8vo, x + 492 pp., 252 figs.

the teacher and student the latest phase in the development of morphological conceptions. No longer is the plant treated as a mere mechanical complex of root, stem, and leaves. Instead it is presented as a living being, plastic in its environment. The work of root, stem and leaves, of the flowers and of the fruit, the influence of the surroundings upon the plant, are discussed in separate chapters, and these matters are made the subjects of extensive experimental investigation. Yet these experiments are simple in the extreme, as is the apparatus, in the construction of which a great deal of ingenuity has been displayed. It is such that any handy, intelligent boy can readily make it.

The primary-school teacher will find this book a valuable adjunct in her work; in the high school and university it can be given directly into the hands of the student, whom it forces to think rather than be content with the absorption of predigested statements.

The last two chapters, the one on plants which cause decay, fermentation, and disease and the other on making new kinds of plants, bring the laboratory more directly in touch with the outer world since they show how man can control diseases on the one hand and the formation of new varieties of fruits and flowers on the other. The introduction of a chapter relating chiefly to the work of Burbank and de Vries, with both of whom Dr. Osterhout is thoroughly acquainted personally, is a distinct innovation as far as botanical text-books are concerned. Then, too, the book deals with those other problems, which more recently have been suggested to the popular mind by newspaper and magazine articles, such problems as the pasteurizing of milk, vaccination and antitoxins, the self-purification of rivers and streams, nitrifying bacteria,— all of them issues of to-day and of great popular interest, interest which will necessarily extend to *Experiments with Plants*.

The book will prove equally acceptable from a purely botanical and from a purely pedagogical standpoint. It is intended to take the place of a similar book the writing of which was projected by Professor Bailey, to complete his series of Botanical Text-books. Certainly no one was better qualified to undertake the work than Dr. Osterhout, whose clear and concise manner of presenting the subject and whose easy, almost colloquial style make the book attractive.

The illustrations are as numerous as they are excellent. Most of them are from original photographs and drawings, a very pleasing feature, since it becomes tiresome to meet again and again the same familiar drawings, however excellent. The bookwork too, deserves

commendation. A fairly large type, good paper, and lack of typographical errors are always appreciated.

Hus

Sargent's Manual.[1]— No other person so well equipped for the description of North American trees as Professor Sargent could have been found, nor an illustrator so expert and practiced as Mr. Faxon; hence it results that no manual of our trees so good as the present could have been expected from any other source. To the makeup of the book the Riverside Press have brought their usual skill. The total result, therefore, is a well devised, well written, well illustrated, and well made book, condensing into convenient size what is necessary for the study of our trees, and yet not skimping the descriptions. As was to be expected, the sequence (after Engler and Prantl) and nomenclature (after Sargent's Silva) are rather radically modern, while the treatment of species is rather conservative except in the daily amplifying genus Cratægus, to which further species are here added.

A synopsis of families with a key based on their leaves renders the first placing of a given form easy, while genera and species are differentiated in the same manner.

If any fault is to be found with the book it will probably be with the absence of synonymy, especially that referring to the new names introduced, except for references to differing names employed in the author's *Silva*.

W. T.

Notes.— Contributions from the Gray Herbarium of Harvard University, n. s., no. 31, published as vol. 41, no. 9, of *Proceedings of the American Academy of Arts and Sciences* under date of July 24, contains "Descriptions of Spermatophytes from the Southwestern United States, Mexico, and Central America," by Greenman, and "Diagnoses and Notes relating to American Eupatoriæ," by Robinson.

A reprint of the original edition of Nuttall's *Journal of Travels into the Arkansas Territory, during the Year* 1819, Philadelphia, 1821, forms vol. 13 of Thwaites' *Early Western Travels*, in course of publi-

[1] Sargent, C. S. *Manual of the Trees of North America exclusive of Mexico.* Boston and New York, Houghton, Mifflin and Co., 1905. 8vo, xxiii + 826 pp., 644 text figs., with map showing the principal tree regions of the United States.

cation by the Arthur H. Clark Company of Cleveland. The editor's preface to the present volume contains an interesting sketch of Nuttall's work.

The 3-volume edition of James' *Account of an Expedition from Pittsburgh to the Rocky Mountains, performed in the Years* 1819, 1820 .... *under the command of Maj. S. H. Long*, London, 1823, forms volumes 14–17 inclusive of Thwaites' *Early Western Travels.*

The third series of *Vegetationsbilder*, by Karsten and Schenck (Jena, Fischer, 1905) presents, thus far, "Flower Gardens of Brazilian Ants," by Ule, "Vegetation of Russian Turkestan," by E. A. Bessey, and the "Vegetation of Java," by Büsgen, Jensen, and Busse.

Professor Peck's "Report of the State Botanist, 1904" forms *Bulletin* 94 (*Botany* 8) *of the New York State Museum*, and bears date July, 1905.

Coste's *Flore descriptive et illustrée de la France* reaches Orchidaceæ in the recently issued fourth fascicle of vol. 3.

Vol. 4, part 3, of Wood's *Natal Plants*, issued in June, contains plates 351–375, with descriptive text.

A revised classification of roses, by Baker, is published in the *Journal of the Linnean Society — Botany*, of July 1.

Miss Eastwood has published a very usable handbook of the trees of California under date of July 8 as *Occasional Papers no.* 9 *of the California Academy of Sciences.* Leaf, fruit, and general character keys make the paper useful, and it is illustrated by 57 plates, partly from nature but largely after drawings by the late Dr. Kellogg.

A revision of Berberis is being published by Schneider in the *Bulletin de l'Herbier Boissier.*

The species of Cratægus of Berks Co., Pa., are considered by C. L. Gruber, of Kutztown, Pa., in three pamphlets, the first two of which were issued by the Berks County Natural Science Club in 1903, while the last appears in the *Bulletin of the Torrey Botanical Club* for 1905.

L. A. Dode has recently issued from vol. 18 of the *Mémoires de la Société d'Histoire Naturelle d'Autun* a monographic account of Populus.

A note on his American observations on the *biennis* group of Œnothera is separately printed by DeVries from the *Album der Natuur.*

Beccari's long-interrupted palm studies have been resumed, and he has recently published several important papers in *Webbia*, issued by Count Martelli of Florence.

Habit photograms of *Sabal palmetto* are given by Nehrling in *Die Gartenwelt* of July 15.

A note on some agaves flowering at Le Martola is published by Berger in *The Gardeners' Chronicle* of August 26.

From tests recorded in *Bulletin no. 72 Bureau of Plant Industry, U. S. Department of Agriculture*, Scofield concludes that the salt water limit of *Zizania aquatica* is approximately represented by 0.03 of the normal solution of sodium chloride,— when the water is not appreciably salty to the taste.

An illustrated paper on the ancestors of the "Big Trees" (Sequoia), by Berry, appears in *Popular Science Monthly* for September.

According to vol. 5, no. 3, of the *Bulletin du Jardin Impériale Botanique de St. Pétersbourg*, the St. Petersburg garden has recently secured three specimens of *Osmunda regalis* over 1000 years old.

Two fascicles (222 and 223) of Engler and Prantl's *Die natiirlichen Pflanzenfamilien*, by Brotherus, dealing with mosses, have recently been issued.

A lecture on diatoms with illustrations, by Mann, is contained in vol. 48, part 1, of *Smithsonian Miscellaneous Collections*.

Regeneration among kelps is considered by Setchell in vol. 2, no. 5, of *University of California Publications — Botany*.

A well illustrated popular account of desert plants is published by Holder in *The Country Calendar* of August.

A paper on the megaspore membrane of the gymnosperms, by Thomson, forms no. 4 of the *University of Toronto Studies, Biological Series*.

Karyokinetic papers of importance occupy vol. 24, part 1, of the *Jahrbücher fur wissenschaftliche Botanik*, issued in July.

The importance of investigations of seedling stages, as presented by Dr. Harris before the St. Louis Congress of 1904, is analyzed in *Science* of August 11.

A paper on seed studies made by Todaro at the Modena agricultural station is published in *Le Stazioni Sperimentali Agrarie Italiane*, vol. 38, fascicle 5–6, with a colored plate showing the tests of dry and viable seeds of Trifolium and Hedysarum.

A paper on the dispersal of seeds by wind is published by Ridley in the *Annals of Botany* for July.

The pollination of *Cypripedium spectabile* by honey-bees is described and photographically illustrated by W. H. Sargent in *Country Life in America* for September.

A paper on the insect galls of Indiana, by M. T. Cook, is published in the *29th Annual Report of the Indiana Department of Geology and Natural Resources.*

A paper on "The Science of Plant Pathology" is published by Stevens in *Popular Science Monthly* for September.

Hedgcock, in *Science* of July 28, reports some of the results of his work with "crown gall" of fruit trees, walnuts, etc.

Some vine diseases in Sonoma County, Cal., are discussed by Butler in *Bulletin no.* 168 *of the Agricultural Experiment Station of the University of California.*

A report on plant diseases of the State, by Sheldon, forms *Bulletin no.* 96 *of the West Virginia Agricultural Experiment Station*, issued on June 30.

A second Hemileia, on orchids, is described and figured by Massee in *The Gardeners' Chronicle* of August 19.

A paper on white rust of the lemon is published by Cavara and Mollica in vol. 17 of the *Atti della Accademia Gioenia di Catania.*

Three new fungi from Catalina Island are described by Ellis and Everhart in the April *Bulletin of the Southern California Academy of Sciences*, which also contains a short article by Blanche Trask on San Jacinto plants.

Nigrosphæria is the name given by Gardner to a new genus proposed for *Sphæria* (*Hypocrea*) *setchellii* Harkness, in vol. 2, no. 6, of *University of California Publications — Botany.*

Thaxter publishes "Preliminary Diagnoses of New Species of Laboulbeniaceæ — VI" as Contributions from the Cryptogamic Lab-

oratory of Harvard University — LXII, in vol. 41, no. 11, of *Proceedings of the American Academy of Arts and Sciences*, issued in July.

Mangin and Viala give an account of *Stearophora radicicola*, a fungus parasite of the roots of Vitis, in the *Revue de Viticulture* of July 6.

Holway has begun the publication of a series of descriptions with photomicrographic illustrations of the North American Uredineæ. The first fascicle, dealing with the Puccinias of Ranunculaceæ, Berberidaceæ, Papaveraceæ, Bromeliaceæ, Commelinaceæ, Juncaceæ, Liliaceæ, Amaryllidaceæ, Iridaceæ, and Orchidaceæ, was issued on the 15th of April.

A paper by Peglian on the Urophlyctis disease of alfalfa is published in vol. 14, no. 12, of *Atti della R. Accademia dei Lincei.*

An illustrated account of the Ustilagineæ of Connecticut, by Clinton, forms *Bulletin no. 5 of the Geological and Natural History Survey* of that State.

An illustrated article on "Mushrooms and Toadstools" is published by Arthur in *The Country Calendar* for September.

A well illustrated preliminary report on the Hymeniales of Connecticut, by White, forms *Bulletin no.* 3 *of the Geological and Natural History Survey* of the State.

An illustrated account of new Citrus creations of the Department, by Webber and Swingle, is separately printed from the *Yearbook of the United States Department of Agriculture for* 1904.

The maple-sugar industry forms the subject of *Bulletin no.* 59 *of the Bureau of Forestry, United States Department of Agriculture,* by Fox and Hubbard.

A paper on red gum (Liquidambar), by Chittenden and Hatt, has recently appeared as *Bulletin no.* 58 *of the Bureau of Forestry, United States Department of Agriculture.*

De Vries describes some of Burbank's methods in *Popular Science Monthly* for August.

An account of Kola in Yoruba Land is given by Bernegau in *Der Tropenpflanzer* for July.

Statistics concerning yerba maté (*Ilex paraguayensis*) are given in *Daily Consular Report No.* 2247, of May 2.

An account of rubber cultivation in Hawaii is given by Smith in *Press Bulletin no.* 13 *of the Hawaii Agricultural Experiment Station*, dated July 20, 1905.

An article on gutta percha, with photograms of Palaquium, is published by Murdoch in *The Indian Forester* of June.

An exhaustive account of the aboriginal use of wood in New York is given by Beauchamp in *Bulletin* 89 (*Archeology* 11) *of the New York State Museum.*

Preliminary accounts of the recent International Botanical Congress at Vienna are given by Rendle in *The Journal of Botany* for July 1 and Britton in *Science* of August 18.

Under the title *Webbia*, Count Martelli has recently issued a volume of botanical papers, by various writers, commemorative of the 50th anniversary of the death of Barker-Webb.

An appreciative sketch of Delpino, by Ludwig, is published in *Naturwissenschaftliche Rundschau* of August 10.

The Journals.— *Botanical Gazette*, July:— Smith, "Undescribed Plants from Guatemala and other Central American Republics — XXVII"; Snow, "The Development of Root Hairs"; Frye and Blodgett, "A Contribution to the Life History of *Apocynum androsæmifolium*"; Nelson, "Contributions from the Rocky Mountain Herbarium — VI"; B[arnes], "The Vienna Congress"; and Florence Lyon, "Another Seed-like Character of Selaginella."

Botanical Gazette, August:— Moore, "Sporogenesis in Pallavicinia"; McCallum, "Regeneration in Plants — I"; Dean, "On Proteolytic Enzymes — II"; Schneider, "Contributions to the Biology of Rhizobia — IV, Two Coast Rhizobia of Vancouver Island, B. C."; Beal, "The Vitality of Seeds"; Rose and Painter, "Some Mexican Species of Cracca, Parosela, and Meibomia"; Greenman, "A New Krynitzkia."

The Bryologist, September:— Chamberlain, "Maryland Bryophytes and Two Mosses from Virginia"; Williams, "Notes on Luzon Mosses"; Holzinger, "*Bryum fosteri*"; Britton, "The Botanical Congress at Vienna"; Sargent, "Lichenology for Beginners — III"; Fink, "What to Note in the Macroscopic Study of Lichens — II"; Gilbert, "The Advantage of Frequent Visits to Moss Localities."

Bulletin of the Torrey Botanical Club, July:— Latham, "Stimulation of Sterigmatocystis by Chloroform"; Murrill, "The Polyporaceæ of North America—XI, a Synopsis of the Brown Pileate Species"; House, "Further Notes on the Orchids of Central New York"; Piper, "The two Eastern Species of Melica"; Gruber, "Cratægus in Berks County, Pennsylvania — III."

Bulletin of the Torrey Botanical Club, August:— Cannon, "On the Transpiration of *Fouquieria splendens*"; Martin, "Studies on the Effect of some Concentrated Solutions on the Osmotic Activity of Plants"; Schneider, "*Chroolepus aureus* a Lichen"; Piper, "*Poa gracillima* Vasey and its Allies."

A small quarterly of miscellaneous contents, has been started by T. J. Fitzpatrick of Iowa City under the title *The Iowa Naturalist.*

Journal of Mycology, May:— Morgan, "A New Chætosphæria"; Lawrence, "Notes on the Erysiphaceæ of Washington"; Ellis and Bartholomew, "Two New Haplosporellas"; Beardslee, "The Rosy-spored Agarics or Rhodosporæ"; Ricker, "Notes on Fungi — II, with New Species from Various Localities"; Bates, "Rust Notes for 1904"; Thom, "Some Suggestions from the Study of Dairy Fungi"; Kellerman, "Index to North American Mycology"; Kellerman, "Notes from Mycological Literature — XV."

Journal of the New York Botanical Garden, August:— MacDougal, "The Suwarro, or Tree Cactus."

Pittonia, part 28:— Greene, "Revision of Eschscholtzia"; "A New Papaveraceous Genus [Petromecon]"; "A Study of Dendromecon"; "Suggestions Regarding Sanguinaria."

The Plant World, June: — Ramaley, "A Botanist's Trip to Java"; Spillman, "Cactus as a Forage Plant."

The Plant World, July:— Reed, "A Brief History of Ecological Work in Botany"; Blodgett, "Fasciation in Field Peas."

Proceedings of the Iowa Academy of Sciences for 1904:— Shimek, "Botany in its Relation to Good Citizenship"; Fink, "Notes on American Cladonias"; Fink, "Some Notes on Certain Iowa Algæ"; Macbride, "The Slime Moulds of New Mexico"; Gow, "An Ecological Study of the Sabine and Neches Valleys, Texas"; Fawcett, "Variation in Ray Flowers of *Anthemis cotula* and other Composites"; Buchanan, "Notes on a Thermophilic Bacillus"; Pammel, "Notes

on the Flora, especially the Forest Flora, of the Bitter Root Mountains"; Seaver, "An Annotated List of Iowa Discomycetes"; Rueda, "The Biology of the *Bacillus violaceus laurentius* or *Pseudomonas janthina*"; Anderson, "Plants New to the Flora of Decatur County, Iowa"; Lindly, "Flowering Plants of Henry County"; Watt, "Growth and Pigment Production of *Pseudomonas janthina*"; Peck, "The Flowering Plants of Hardin County."

Proceedings of the Society for the Promotion of Agricultural Science, 26:— Bailey, "What is Horticulture?"; Lazenly, "The Economic Uses of Wood"; Pammel, "Some Fungus Diseases Common in Iowa During the Season of 1904"; Beal, "The Vitality of Seeds"; Arthur, "The Part taken by Teleutospores and Æcidia in the Distribution of Maize and Cereal Rusts."

Rhodora, August:— Shear, "Letter of Dr. Asa Gray to Lewis D. de Schweinitz"; Blanchard, "The Yellow-fruited Variety of the Black Raspberry"; Fernald, "The Genus Arnica in Northeastern America," "*Spergula sativa* in Connecticut," "Some Lithological Variations of Ribes," and "*Anaphalis margaritacea* var. *occidentalis* in Eastern America"; Ballard, "A Second Vt. Station for *Arenaria macrophylla*."

Torreya, July:— Schneider, "An Example of Complex Life-relationship"; Christ, "Quelques mots sur l'article de Mr. Underwood 'A much Named Fern'"; Greene, "Derivation of the Name Chamæcrista"; Harper, "Two Misinterpreted Species of Xyris."

Torreya, August:— Coker, "Observations on the Flora of the Isle of Palms, Charleston, S. C."; Cockerell, "Names of Insects"; Hanmer, "A Note regarding the Discharge of Spores of *Pleurotus ostreatus*."

GEOLOGY.

Notes.— *Water Supply and Irrigation Papers*, 97, 98, 99, *and* 100, form the report of the branch of the Division of Hydrography dealing with stream measurements for the year 1903. These four reports represent over fifteen hundred pages of valuable data, collected from almost all the important streams of the United States. The results have been compiled by J. C. Hoyt, under the direction of F. H. Newell.

The relation between rainfall and run-off, under different climatic conditions, is very clearly brought out in many of the tables.

The "Report of Progress of Stream Measurements for the Calendar Year 1904" forms *Water Supply and Irrigation Papers* 124–135 inclusive. The various portions of the country are treated in the separate bulletins, as follows:—

124, Pt. 1, Atlantic Coast and New England Drainage.
125, " 2, Hudson, Passaic, and Delaware River Drainages.
126, " 3, Susquehanna, Patapsco, Potomac, James, Roanoke, Cape Fear, and Yadkin River Drainages.
127, Pt. 4, Santee, Savannah, Ogeechee, and Altamana Rivers, and Eastern Gulf of Mexico Drainage.
128, Pt. 5, Eastern Mississippi River Drainage.
129, " 6, Great Lakes and St. Lawrence River Drainage.
130, " 7, Hudson Bay, Minnesota, Wapsipinicon, Iowa, Des Moines, and Missouri River Drainages.
131, Pt. 8, Platte, Kansas, Meramee, Arkansas, and Red River Drainages.
132, Pt. 9, Western Gulf of Mexico and Rio Grande Drainages.
133, " 10, Colorado River and the Great Basin Drainages.
134, " 11, The Great Basin and Pacific Ocean Drainage in California.
135, Pt. 12, Columbia River and Puget Sound Drainages.

A new term applying to veins, namely "rift-veins," is proposed by J. A. Reid, in a paper entitled "The Structure and Genesis of the Comstock Lode" (*University of California, Bulletin of the Department of Geology*, vol. 4, no. 10, pp. 177–199). The type of this kind of vein is the Comstock, where "the surface 'east vein,' the famous bonanza, and the 'vein' now being worked have an identical origin. Their formation lies in the fact that the lower part of the hanging wall block has settled more than the upper, relative to the foot wall, and has been torn apart by the stresses developed."

The *Journal of Geology* for July–August, 1905, contains the following articles: "The Geographical Cycle in an Arid Climate," by W. M. Davis; "Notes on Baked Clays and Natural Slags in Eastern Wyoming," by E. S. Bastin; "The Delaware Limestone," by C. S. Prosser; "*Megacerops tyleri*, a New Species of Titanothere from the Bad Lands of South Dakota," by R. S. Lull; "Comment on the 'Report of the Special Committee on the Lake Superior Region,'" by A. C. Lane.

"The Lead, Zinc and Fluospar Deposits of Western Kentucky," by E. O. Ulrich and W. S. T. Smith, forms *Professional Paper* no. 36 of the United States Geological Survey. The general geology of the district is treated by Ulrich, while the detailed description of the different deposits is by Smith. Smith regards the fluorite as having been deposited from circulating underground waters, and having been derived, probably, from the limestones of the region. On noticing the number of faults and dikes that have been mapped in this region, one questions why a deep-seated source of the fluorite is regarded untenable.

The character of the triclinic feldspars at high temperatures has recently been investigated by Messrs. Day and Allen. The careful measurements of the melting points, points of crystallization, specific gravities, etc., all prove that in triclinic feldspars, isomorphism is complete. The slides prepared from the various feldspar mixtures were examined by J. P. Iddings, and he found that, optically, the feldspars correspond very closely to the mixtures prepared. The optical portion of the paper is illustrated by six remarkably clear plates. This report is entitled "The Isomorphism and Thermal Properties of the Feldspars," and is published by the Carnegie Institution of Washington, as *Publication* no. 31.

An exhaustive description of the Bingham District of Utah has been prepared by Boutwell, Keith, and Emmons. This report, which is published as *Professional Paper* no. 38 of the United States Geological Survey, consists of four parts. The first part is a general presentation of the problem by Emmons. The second part is by Keith, and treats the areal geology of the region. The third, and by far the most important portion of the monograph, is by Boutwell. The successive stages of oxydation are well shown by the fact that in the surface zone free gold, some oxides, and carbonates were found; on descending, a zone of carbonates occurred, with a little sulphide; while, at a greater depth, the sulphides became more and more abundant until the carbonate and oxide ores have given place almost entirely to sulphides, of which the copper sulphide is most important, economically. The fourth portion of the report is an appendix describing the fossils of the Bingham District, by Girty.

Professional Paper no. 34 of the United States Geological Survey, "The Delavan Lobe of the Lake Michigan Glacier of the Wisconsin Stage of Glaciation and Associated Phenomena," by W. C. Alden,

is a detailed study of southern Wisconsin and northern Illinois. The report is fully illustrated by maps, representing the successive stages in the deglaciation of the district.

Publication 101 of the Field Columbian Museum, entitled "The Rodeo Meteorite" by O. C. Farrington, is a description of a medium octahedrite with high phosphorus content, weighing about one hundred pounds. The mass was found in 1852, in the State of Durango, Mexico.

A series of experiments which aim to give some quantitative values for the pressures exerted by growing crystals, has been performed by G. F. Becker and A. L. Day. In these experiments, it has been proved that crystals increase most rapidly on their under surfaces, and thus lift the earlier formed portions. So energetic is this action that a kilogram weight was raised several millimeters by an alum crystal whose bearing surface was only a small fraction of a square centimeter. The force, therefore, is believed to be of the same order of magnitude as the resistance that crystals offer to crushing. The published account of these experiments appears in the *Proceedings of the Washington Academy of Sciences*, vol. 7, pp. 283–288.

P. S. S.

(No. 469 was issued January 20, 1906)

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THE AMERICAN NATURALIST

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CONTENTS

		Page
I.	Notes on Reptiles and Batrachians of Pennsylvania, New Jersey, and Delaware . . . . . W. STONE	159
II.	Anatomy of *Acmæa testudinalis* Müller. Part I. Introductory Material — External Anatomy . . . . . PROFESSOR M. A. WILLCOX	171
III.	Affinities of Certain Cretaceous Plant Remains Commonly referred to the Genera Dammara and Brachyphyllum DR. A. HOLLICK AND PROFESSOR E. C. JEFFREY	189
IV.	A New Pycnogonid from the Bahamas . . . . . L. J. COLE	217
V.	Additional Notes on Bahama Snakes . . . . . T. BARBOUR	229
VI.	Publications Received	233

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THE

AMERICAN NATURALIST

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NOTES ON REPTILES AND BATRACHIANS OF PENNSYLVANIA, NEW JERSEY AND DELAWARE

WITMER STONE

IN view of the increasing interest in the study of our reptiles and batrachians it seems desirable to place on record any facts that may add to our knowledge of the distribution and relative abundance of the various species. The writer therefore offers the following list which is based upon his personal observations in eastern Pennsylvania and southern New Jersey, and upon specimens contained in the splendid collection of the Academy of Natural Sciences of Philadelphia, which includes the collections of Green, Hallowell, A. E. Brown, and Cope, together with local material collected by Samuel Ashmead, Samuel N. Rhoads, Henry W. Fowler, and the writer.

No species are included unless specimens obtained in one of the three States have been examined, and unless otherwise stated the specimens are in the Academy collection.

It follows that a few species which have been recorded from the district under consideration but of which no specimens were accessible have been omitted, and as the notes are only intended as a contribution toward a complete list, no attempt has been made to quote records or observations at second hand. Further collections will undoubtedly extend the range of many species.

Necturus maculosus Rafinesque.—One specimen obtained in

Darby Creek near Essington, Delaware Co., Pa., by Jas. Gardiner, March 2, 1900, is the only example I have ever seen from this vicinity.[1]

Cryptobranchus alleghaniensis (Daudin). —Mainly west of the Alleghanies. Specimens examined from the Beaver and Alleghany Rivers and also from the Susquehanna near Tucquan, Lancaster Co., where it was occasionally taken by the late Jacob Stauffer, of Lancaster, Pa.

Amblystoma opacum (Gravenhorst).— I have never personally collected this species but have examined specimens from

New Jersey, Atlantic City (W. J. Fox), Beesley's Point (Ashmead), and Medford (J. S. Wills);

Delaware, Newark (T. B. Wilson).

Amblystoma punctatum (Linné).—Occasional but not an abundant species.

Pennsylvania, Philadelphia (J. W. Tatum), Ardmore, Mont. Co. (I. N. De Haven), Clifton, Delaware Co. (B. Wainwright), York Furnace, York Co. (Stone), Chambersburg (Rhoads).

Amblystoma conspersum Cope.—Cope's type specimen from Londongrove, Chester Co., Pa., is the only one I have seen from this district.

Amblystoma bicolor (Hallowell).— I have seen only the type specimen from Beesley's Point, N. J.

Amblystoma tigrinum (Green).—Specimens have been examined from Beesley's Point, N. J. (S. Ashmead, G. H. Horn), and from Crosswicks, N. J. (J. H. Slack). I have never taken it in Pennsylvania.

Amblystoma jeffersonianum (Green).—One specimen in the Academy collection was obtained by Dr. Hallowell "near Philadelphia." I know of no other captures.

Hemidactylium scutatum (Schlegel).— Five specimens were obtained by S. N. Rhoads at Swartzwood Lake, Sussex Co., N. J., in October, 1895, and another from the same County a year later.

Plethodon cinereus (Green).— An abundant species about Philadelphia ranging to the highest parts of the Pennsylvania Alleghanies,—Ganoga Lake, Sullivan Co. (S. Brown)—and to Swartz-

[1] *Cf.* Fowler, *Science*, (n. s.), vol. 11, p. 555, 1900.

wood Lake, northern New Jersey (Rhoads). I have also taken it in Delaware and have examined specimens from as far south as Seaford in that State.

It has always been my experience that this and the following species are nowhere equally abundant; one or the other always predominates.

Plethodon glutinosus (Green).—I have never taken this salamander about Philadelphia or in southern New Jersey, and it seems to be a characteristic species of the mountains or their foothills.

I have examined specimens from the following localities:—

Pennsylvania, Warren Co. (Dr. Kennedy), Venango Co. (Miss Brown), Huntingdon Co. (Dr. Leidy), Juniata Co., York Co., Sullivan Co., Pike Co.

New Jersey, Swartzwood Lake, Sussex Co. (Rhoads).

Gyrinophilus porphyriticus (Green).—This is also a mountain species, and has never so far as I am aware, been taken within the limits of the Carolinian fauna. I have examined the following specimens:—

Pennsylvania, Warren Co. (Dr. Kennedy), Altoona, Blair Co. (Dr. Leidy), Round Island, Clinton Co. (Rhoads), and Tuscarora, Juniata Co. (C. Ingersoll).

Spelerpes bilineatus (Green).—This is a rather common and widely distributed species. I have taken it at various points in Philadelphia, Chester, and Lancaster Co., Pa., as well as in southern New Jersey west of the pine barrens. I have also examined specimens from Atlantic City, N. J., and from Morris Co. (F. Canfield), Swartzwood Lake and White Pond (Rhoads) in the northern part of the State and from Dingman's Ferry, Pike Co., Pa. (Rhoads).

Spelerpes longicauda (Green).—This species is not so plentiful as the preceding and I have never taken it in the southeastern part of Pennsylvania nor in southern New Jersey although there is one in Cope's collection from Atlantic City, N. J.

Farther west in Pennsylvania I have examined specimens from Lancaster Co., Huntingdon Co. (Cope), Cresson, Blair Co., and Round Island, Clinton Co. (Rhoads). In northern New Jersey Rhoads obtained it at White Pond, Warren Co.

Spelerpes ruber (Daudin).—A common species in spring heads. I have taken it in Philadelphia, Chester, and Lancaster Cos., and in Camden Co., N. J. It seems fairly well distributed and has been obtained in the Alleghanies at Round Island, Clinton Co. (Rhoads), and in Blair Co. (Dr. McCook); also at Wilmington, Delaware. I fail to distinguish the variety *montanus* Cope.

Desmognathus ocrophæa Cope.—This seems to be a boreal species and I have only seen specimens from the higher Alleghanies, Harvey's Lake, Luzerne Co. (Stone), Lake Ganoga, Sullivan Co. (Rhoads), and Clinton Co., Pa. (S. Brown).

Desmognathus fusca (Rafinesque).—Probably our most abundant salamander. Found throughout eastern Pennsylvania, northern and southwestern New Jersey, but apparently not in the streams of the pine barrens. In Delaware it occurs in the Brandywine drainage and probably elsewhere.

Desmognathus nigra (Green).—The only Pennsylvania specimen that I have seen is one presented to the Academy by Dr. Holbrook without definite locality.

Diemyctylus viridescens Rafinesque.—An abundant species in the lakes and ponds of the mountainous parts of Pennsylvania and New Jersey; the terrestrial form is common in the hemlock forests.

I have taken it sparingly in York and Chester Cos., but not about Philadelphia nor in southern New Jersey, though Dr. Wilson obtained some near Newark, Delaware.

Bufo lentiginosus americanus (Holbrook).—Everywhere abundant from the mountains to the coast, including the pine barrens.

Acris gryllus crepitans Baird.—I have found this species common along the lower Delaware and Susquehanna valleys. H. W. Fowler has secured it at Cape May, N. J., and S. N. Rhoads obtained it in Sussex, Somerset, and Warren Cos., in the upper part of the State.

Chorophilus triseriatus Wied.—Personally I have not observed this frog but Cope states that it is common in southwestern New Jersey and he also observed it in southern Chester Co., Pa. Rhoads obtained specimens at Pine Grove, Cumberland Co., Pa.

Hyla versicolor Le Conte.—This is the most frequent tree frog during the summer, for the others are seldom seen except when

gathered in the ponds, in springtime. It is quite generally distributed south of the mountains, the most northern specimen that I have examined being from Morristown, N. J. (M. Fisher).

Hyla pickeringii Holbrook.— A common species in shaded pools in early spring. I have examined specimens from the Delaware valley, Chester Co., Pa., and also from Altoona, Blair Co., Pa. (Dr. Leidy), and Pine Grove, Cumberland Co. (Rhoads). Dr. Wilson obtained it in Delaware.

Hyla andersonii Baird.— All the specimens so far secured except the type have come from the pine barren region of New Jersey. Dr. Leidy's specimen from Jackson and one obtained by Mr. H. L. Viereck[1] at Clementon are in the Academy's collection. The others were two secured at Pleasant Mills by Dr. J. P. Moore and one from May's Landing, (J. E. Peters).

Rana pipiens Schreber.— Abundant all along the coast marshes and large rivers. I have examined specimens also from White Pond, N. J., and Waynesburg, Green Co., Pa. (Rhoads), and from several cedar swamps in the New Jersey pine barrens. In the latter region *R. palustris* does not seem to occur.

Rana palustris Le Conte.—Common throughout Pennsylvania and in northern and southwestern New Jersey. It ranges to the top of the Alleghanies as I have seen it in Sullivan and Wyoming Cos., and Rhoads took it at Round Island, Clinton Co., Pa.

Rana sylvatica Le Conte.— Distributed throughout Pennsylvania and New Jersey. I have found it on the highest ranges of the Alleghanies and on the edge of the pine barrens at Medford, N. J., while Rhoads secured a specimen at May's Landing, in the same State.

Rana clamitans Latreille.— Abundant and widely distributed, occurring both in the mountains and in the pine barrens of New Jersey where it is the most abundant frog.

Rana catesbiana Shaw.— Apparently widely distributed but much scarcer than formerly. I have taken it on the lower Delaware and Susquehanna and their tributaries and have seen specimens from Absecon, N. J. (S. Ashmead), and Harvey's Lake, Pa.

[1] Stone, *Proc. Acad. Nat. Sci. Phila.*, 1901. Since this paper was prepared, W. T. Davis has discovered this species and *Rana virgatipes* at Lakehurst in the New Jersey pine barrens (*Amer. Nat.*, vol. 38, p. 893; vol. 39, p. 795).

Rana virgatipes Cope.— All of the specimens of this interesting frog that have been captured, are, so far as I am aware, in the Academy's collection and have been fully reported upon by H. W. Fowler.[1] They are all from the New Jersey pine barrens; the one obtained by the writer was from Speedwell, Burlington Co.

Carphophiops amœnus (Say).—Obtained in Chester and York Cos., Pa., and Pt. Pleasant, Beesley's Point (Ashmead), Trenton (Abbott), and Bridgeton (Walmsley), N. J.

Virginia valeriæ Baird & Giraud.—One specimen is in the Academy collection from Delaware received from C. Drexler.

Storeria occipitomaculata (Storer).— A common snake throughout the mountains south of the Pocono plateau and east of the Alleghanies. I have only seen one example which I captured in the New Jersey pine barrens on the edge of Bear Swamp, east of Medford. This record is interesting as in the same vicinity we find Evotomys, a northern rodent, common in the mountains, but absent in the intervening territory.

Storeria dekayi (Holbrook).— A rather common snake in southeastern Pennsylvania; also obtained at May's Landing, N. J., and doubtless of wider distribution in both States.

Clonophis kirtlandi (Kennicott).—Two examples from the region under consideration are in the Academy collection; one obtained near Trenton, N. J., by Dr. C. C. Abbott, the other in Delaware Co., Pa., by E. Dutton.

Tropidoclonium lineatum Hallowell.— A snake was obtained at Round Island, Clinton Co., Pa., by Seth Nelson collecting for Mr. S. N. Rhoads, which he identified as this species. I examined it at the time and I have no doubt as to the correctness of the identification. Unfortunately the specimen cannot now be found.

Thamnophis sauritus (Linné).—This is a rather common snake throughout the lowlands and probably the mountains also. I have seen specimens from the Pocono plateau, Pa., and Swartzwood Lake, N. J., but not as yet from the main Alleghany range.

Thamnophis sirtalis (Linné).—The Garter Snake is distributed

[1] *Proc. Acad. Nat. Sci. Phila.*, p. 662, 1905.

all over the region under consideration and presents several more or less distinct types of coloration. So far as the material available for examination is concerned it would seem that the dark form with the stripes nearly obliterated, *T. s. ordinatus*, is restricted to the higher Alleghanies as the only specimens are from Sullivan and Wyoming Cos. (Stone) and Port Alleghany, McKean Co. (Fowler). All the specimens that I have seen from south of the mountains are true *sirtalis* with well defined stripes and usually conspicuous spots. Those obtained by Rhoads at Round Island, Clinton Co., Pike Co., Pa., and Sussex Co., N. J., are somewhat intermediate. That these two forms are not absolutely coincident with the Canadian and Carolinian-Alleghanian belts as indicated, is shown by the fact that a fairly typical *sirtalis* was obtained on the high Alleghanies of Sullivan Co., Pa A nearly uniform green specimen, "*T. s. gramineus*" Cope, was also obtained at the latter locality. This I take to be a mere color form of *ordinatus*.

Thamnophis butleri Cope.—While for some years *Thamnophis brachystomus* Cope has been regarded as a mere abnormal example of *T. sirtalis*, the recent discovery of a number of specimens in Michigan[1] seems to establish its distinctness. The type is from Franklin, Venango Co., Pa. (Miss A. M. Brown) and I am now able to record an additional Pennsylvanian specimen obtained at Port Alleghany, McKean Co., Aug. 19, 1904, by H. W. Fowler. This individual has the plates as follows: upper labials, 6–6; lower labials, 6–7; postoculars, 2–2; gastrosteges, 136; urosteges, 47; length, 377 mm. It presents the principal additional characteristics of the species in a marked degree, *i. e.*, the rapid tapering toward both head and tail, and the very slight constriction at the neck. The lateral stripe is mainly on the third row of scales involving part of the second and at some points part of the fourth row.

After the above was written Alex. G. Ruthven examined the two specimens and pronounces them in his opinion identical with *T. butleri* a conclusion which he had already reached in connection with Dr. Clark's specimens.[2]

[1]H. L. Clark. *Proc. Biol. Soc. Wash.*, vol. 16, pp. 83–88, 1903.

[2]*Biol. Bull.*, vol. 7, no. 5, Nov., 1904.

Regina leberis (Linné).—This does not appear to be a common species and I have never seen it alive. Two specimens marked "Pennsylvania" (J. L. Wortman) are in the Academy collection as well as specimens from Philadelphia (J. E. Ives), Waynesburg, Green Co., Pa. (Rhoads), and Newark, Del. (Dr. T. B. Wilson).

Natrix sipedon (Linné).—Common in suitable localities throughout the region.

Calopeltis obsoletus (Say).—I have only taken this snake in Chester Co., Pa., but have examined several from southern New Jersey, one of which was obtained on the coast at Stone Harbor, by D. McCadden.

Calopeltis obsoletus confinis Baird & Giraud.—One young specimen secured many years ago at Dennisville, Cape May Co., N. J., by Samuel Ashmead is in the Academy collection, and another was secured at Diamond Valley, Huntingdon Co., Pa., September, 1905, by J. A. G. Rehn. While currently referred to this form it seems probable that these are nothing more than young *obsoletus* which at this age may be highly colored, but so far as I know there is no description of the young of this species. The specimens before me are gray with brown spots.

Opheodryas æstivus (Linné).—I have taken this in the southern part of New Jersey only, and have seen no specimens from elsewhere in the district under consideration. It is locally rather plentiful.

Liopeltis vernalis (DeKay).—A common species throughout the Pennsylvania mountains, McKean Co. (Fowler), Sullivan and Wyoming Cos. (Stone), Clinton Co. (Rhoads), Monroe Co. (C. T. Sands). The only New Jersey example that I have seen was taken at Trenton, N. J., by Dr. C. C. Abbott.

Bascanion constrictor (Linné).—Common in the low grounds and at least onto the first ridges of the mountains and though I have not as yet seen a specimen from the main Alleghany range, it no doubt occurs there.

Pituophis melanoleucus (Daudin).—The commonest large snake in the New Jersey pine barrens but I have not seen specimens from farther north in the State nor from Pennsylvania.

Diadophis punctatus (Linné).—Sparingly about Philadelphia but more plentiful nearer to the mountains, over which it ranges. Specimens examined from

Pennsylvania, Bucks Co. (W. A. Shryock), Cumberland Co. (Rhoads), Lancaster Co. (Stone), Monroe Co. (Rhoads), Harvey's Lake, Luzerne Co. (Stone);

New Jersey, Morris Co. (Dr. Fisher).

Lampropeltis getulus (Linné).—A rather common species in southern New Jersey, the most northern record being Pt. Pleasant, Ocean Co. (S. Brown). All the specimens I have examined came from the eastern and western edge of the pine barrens rather than from the heart of the region though this may have been accidental. Rhoads obtained this snake at Seaford, Del., but I have never seen a specimen from Pennsylvania.

Lampropeltis doliatus (Linné).—One typical specimen from Delaware (J. Green) is in the Academy collection and another not quite typical from the same State obtained by Drexler.

Throughout the greater part of eastern Pennsylvania and New Jersey is found *L. d. clericus* and it is everywhere a common snake unless it be in the New Jersey pine barrens from which district I have seen no specimens. Another race, *L. d. triangulus* (Boie), seems to be the form of the higher mountains and is represented in the Academy collection by a specimen from McKean Co., Pa. (Fowler) and one marked near Philadelphia. More material will be necessary in order to ascertain whether these two forms are constant and confined to the districts assigned to them. Certain it is that examples from twenty localities south of the mountains are all *clericus*, the Philadelphia specimen above mentioned being the only exception.

Heterodon platyrhinos Latreille.—Common, ranging from the Alleghanies across to the coast.

Agkistrodon contortrix (Linné).—Becoming scarce in thickly settled districts. I have seen it in York and Fulton Cos., Pa., and have examined specimens from Carbon Co. (Rehn), Lehigh Co. (Rehn), Pottsville (C. T. Hughes), Round Island, Clinton Co. (Rhoads), Pa. I have seen no specimens from New Jersey.

Crotalus horridus (Linné).—I have found this species within the past few years on the foothills of the main Alleghany Mountains near Lovelton, Wyoming Co., and on Tuscarora Mt., Fulton Co., Pa., while Rehn collected several in Huntingdon Co. and Rhoads obtained specimens at Round Island, Clinton Co., and

in Pike Co., Pa., and I have examined additional specimens from Chambersburg (Mrs. P. P. Calvert) and Warren Co., Pa. (Dr. Slack). In the southeastern parts of the State it is exterminated. In southern New Jersey it is very rare and I know of no authentic recent records though there is a specimen in the Academy collection collected many years ago at Pemberton, N. J. (Dr. Coleman).

Eumeces fasciatus (Linné).—I have taken this lizard at York Furnace, York Co., Pa., and J. A. G. Rehn obtained it on the mountains of Huntingdon Co., Pa., where one would rather expect *E. anthracinus*, a species which I know from the State only on the strength of Baird's Carlisle record. In New Jersey it occurs at May's Landing, Jones Mill, and doubtless other spots in the pine barrens. In Delaware I have found it about Choptank Mills. One in the Wagner Institute collection, captured in Fairmount Park, Philadelphia, a few years ago, may have escaped from confinement like the specimens of Phrynosoma and Alligator which are occasionally found within the city limits.

Leiolepisma laterale (Say).—On September 2, 1901, J. A. G. Rehn and I caught one of these little lizards and saw another a mile or so east of Atsion, Burlington Co., N. J., in the heart of the pine barrens. Dr. J. P. Moore had previously taken it at Pleasant Mills some ten miles farther south.

Sceloporus undulatus (Daudin).—Abundant all over the pine barrens of New Jersey, but I have not seen it from north of this region. In Pennsylvania it is rare, though formerly more common. I have only taken it along the lower Susquehanna valley, in York and Lancaster Cos., though Rhoads obtained it at Round Island, Clinton Co., and I have examined a specimen collected in Chester Co. by Cope.

Dermochelys coriacea (Vandelli).—One was washed ashore at Asbury Park, N. J., some years ago, and another from Delaware Bay is in Cope's collection.

Aspidonectes spinifer (Le Suer).—A few of these turtles have of late years found their way into the Delaware valley. One was captured in Cooper's Creek, N. J., in 1902, and another in Warren Co., N. J., now in the Wagner Institute collection, Philadelphia. I have also examined specimens from the Alleghany River in western Pennsylvania.

Chelydra serpentina (Linné).—Widely distributed throughout the region.

Kinosternon pennsylvanicum (Bosc.).—I have so far found this species only in southeastern Pennsylvania and southern New Jersey, ranging as far north as Sea Girt (Rhoads).

Aromochelys odoratus (Latreille).—Apparently more abundant than the preceding and of wider range. I have seen it from the same general region as the above and also from Swartzwood Lake, Sussex Co., N. J. (Rhoads).

Graptemys geographicus (Le Suer).—I found a carapace and plastron of this turtle on the marsh at Bayside, N. J., in the spring of 1903.

Malaclemmys centrata (Latreille).—I have examined specimens from Cape May, N. J. (Dr. Ruschenberger) and the coast of Delaware but have only one recent record, a specimen in the Wagner Institute collection in Philadelphia, captured in Dias Creek, Cape May Co., N. J., a few years ago. It has become rare within the district under consideration.

Pseudemys rubriventris (Le Conte).—I have seen this turtle in ponds and slow streams at several points in southern New Jersey, especially at Medford and Milford and have examined specimens obtained at Woodbury and Rehoboth Beach, Delaware (T. R. Peale). One in the Academy collection is marked "Delaware River, Philadelphia."

Chrysemys picta (Hermann).—This species is abundant in most large streams and ponds throughout the district though I have no data upon its occurrence on the Alleghanies.

Clemmys muhlenbergi (Schweigger).—I have seen probably a dozen specimens of this turtle in W. Bradford township, Chester Co., Pa., and several in Tinicum, Delaware Co. In New Jersey I secured one at Medford, May 30, 1905, and found another near Audubon, Camden Co., in December. The only other specimens that I have examined were labeled "near Philadelphia."

Clemmys insculptus (Le Conte).—Apparently wide ranging but not very common. I have taken it in Chester and Fulton Cos., Pa., and have examined the following additional specimens: Bristol, Pa. (Fowler), Round Island, Clinton Co., Pa. (Rhoads), Delaware Gap, Warren Co., N. J. (Rhoads), and Woodbury, N. J. I have no record for the pine barrens.

Clemmys guttatus (Schneider).—All over southeastern Pennsylvania and southern New Jersey, including the pine barrens but as to its occurrence in the higher mountains I am in doubt.

Terrapene carolina (Linné).—Common throughout southeastern Pennsylvania especially in Chester Co., and also in the southwestern part of the State, Waynesburg, Green Co. (Rhoads). For New Jersey my data are meager but I have no record for the pine barrens. The species seems to be restricted to the Carolinian fauna. Two specimens of *T. triungius* Agassiz are in the Academy collection labeled "*Cistudo clausa*, near Philadelphia, S. G. Worth." The labels must surely have been transposed as this is quite beyond the range of the species.

ANATOMY OF *ACMÆA TESTUDINALIS* MÜLLER

PART I. INTRODUCTORY MATERIAL—EXTERNAL ANATOMY

M. A. WILLCOX

Introduction

Some months ago I published in this journal under the title "Biology of *Acmæa testudinalis* Müller" an excerpt from a monograph of this species upon which I have long been engaged. I have now decided to publish the entire monograph in sections of which the present is the first. It should naturally be introduced by remarks upon the scope of the work but as these were prefixed to the earlier article, I refer the reader to that, adding merely that the investigation is intended not only as a contribution to a knowledge of the New England fauna but also as a first step in such a careful comparative study of the different species of the genus as is there suggested. This being its aim, it occupies itself in the main with anatomy, touching only incidentally upon either histology or embryology. I have, moreover, tried to make a paper which would serve as an introduction to the study of the neglected but fascinating group of Gastropoda. This aim will, I trust, serve as excuse for the admission of some material too elementary to be included in a paper addressed exclusively to specialists.

Zoölogical Position of Acmæa and its Allies

Acmæa belongs to the Scutibranchiata (Aspidobranchia, Diotocardia of Bouvier *et al.*), a suborder which includes all the more primitive Prosobranchiata and which is divisible into two sections: the Rhipidoglossa (Diotocardia of Remy Perrier) and the Docoglossa (Heterocardia). The only characteristics by which members of these two sections may infallibly be distinguished are first, the nature of the radula and second, the presence of dialy-

neury in the nervous system of the Rhipidoglossa and its absence in the Docoglossa. Dialyneury, it will be remembered, is the name applied to that form of nervous system in which the mantle is innervated in part from the pleural and in part from the visceral ganglia and in which these two systems of nerves are connected by anastomosis. It may be added that the ventricle in Rhipidoglossa is usually traversed by the rectum although the Helicinidæ, which have but one auricle, are an exception to this rule.

The Rhipidoglossa fall into two subsections: the Zygobranchia, characterized by the possession of two gills and two auricles, which are usually symmetrically disposed, although one gill may be smaller than the other; and the Azygobranchia with but one gill and ordinarily with two auricles, one of which is more or less rudimentary or even absent altogether. The Docoglossa have a single gill (ctenidium) or none at all, a single auricle with no trace of a second,[1] and a heart whose ventricle is never traversed by the rectum. It is thus evident that the three divisions of Scutibranchiata form in many respects a continuous anatomical series whose members, whatever the view as to their phylogenetic relationship, may often be profitably compared.

The Docoglossa[2] include three families: the Lepetidæ, Acmæidæ, and Patellidæ. The Lepetidæ is a small family whose members inhabit water of considerable depth. Of its fourteen species and varieties only one is recorded as living at low-water mark; the others have been dredged at depths varying from ten fathoms (five fathoms in one instance) to thirteen hundred ninety-five fathoms. While in certain respects, as in the shell and radula, they exhibit relationship to the Rhipidoglossa, in others they are modified in correlation with their environment so that they appear to be, as maintained by Dall, less typical Docoglossa than are the others. The family contains three genera: Lepeta, (including Pilidium), Propilidium, Lepetella.

The two remaining families are much larger and are typically

[1] Spillmann (:05, pp. 569–571) considers that he has found traces of a second auricle.

[2] In the classification of the Docoglossa I follow Pilsbry (Tryon and Pilsbry, '91).

litoral animals. The first one, the Acmæidæ, comprises those limpets which retain the primitive gill (ctenidium) with or without a cordon of branchial leaflets; the second, the Patellidæ, comprises those which lack a ctenidium but have a branchial cordon. The Acmæidæ contains three genera: Pectinodonta, with one species, a deep-sea form found off some of the West Indian islands; Acmæa, with eighty-four species, of almost world-wide distribution; Scurria (including the subgenus Lottia), whose five species are found only on the West American coasts, as far north as San Francisco. The Patellidæ contains also three genera: Patella (including the subgenus Helcion and the sections Patina, Scutellastra, Ancistromesus, all often regarded as genera), with forty-eight species which with one exception (*P. mexicana*) are entirely restricted to the Old World; Nacella, whose seven species are found only in the region about the southern part of South America; Helcioniscus, with forty-eight species in various portions of the Indian and Pacific Oceans but not extending on the American coast farther north than Chili.

History of Investigation

The name *Patella* (*Acmæa*) *testudinalis* first appears in 1776 in Müller's *Prodromus* but more than fifty years went by before any record was made of so obvious a feature in its anatomy as the possession of a ctenidium. It was the observation of this fact which led Eschscholtz to establish in 1830 the new genus Acmæa. As is well known, his early death left uncompleted the *Zoologischer Atlas* which was to have embodied the results accumulated during the years of his circumnavigating voyages. Such material as was in condition to be used by another was completed by his friend Rathke and published in 1833 as a fifth part of the *Atlas*. It contained an anatomical account, covering two folio pages, of the new genus Acmæa followed by brief descriptions, dealing with only the shells, of eleven species collected by Eschscholtz in the neighborhood of Sitka.

This first anatomical study is purely description and is of merely historic interest. The points touched upon are only the more

obvious ones; the account contains some unquestionable errors and some statements which if correct, do not apply to all members of the genus.

A step in advance was marked by Dall's successive papers on the limpets of which the first appeared in 1869. These papers deal mainly with the Acmæidæ and although preëminently systematic, contain occasionally anatomical facts of interest and importance.

The first considerable contributions to the morphology of Acmæa are contained, however, in two papers on the comparative anatomy of certain organs of Prosobranchs which issued from the laboratory of Professor E. Perrier about fifteen years ago. The first of these papers, (Bouvier, '87) dealt with the nervous system; the second, (Bernard, '90) with the pallial organs. Bouvier ('87, pp. 15–22) gives a full and careful description of the nervous system of Patella and in a single paragraph compares therewith the very similar one of *A. testudinalis*. Bernard describes in detail the osphradium and the innervation of the gill in a species of Tectura (Acmæa) and in the same connection figures and describes the arrangement of the principal ganglia in what he calls *T. fontainesi*. It should be noted that this latter species is without doubt, as I have shown elsewhere, (Willcox, 00) incorrectly named and that the identification of the other, so far as concerns the species, is questionable. The so called *Tectura fontainesi*, having circumpallial branchial lamellæ (Bernard, '90, p. 217) is of course not a true Tectura (Acmæa) but may very probably be a Scurria. *T. pileopsis*, Bernard's other species, is stated by him ('90, p. 217) to have come from Chili but that species is recorded by Pilsbry (Tryon and Pilsbry, '91, p. 57) as belonging to the New Zealand, Indo-Pacific, and Australian region.

The first work in which Acmæa was treated monographically was Haller's *Studien über docoglosse and rhipidoglosse Prosobranchier*, which appeared in 1894. This deals with one species of Scurria and three of Acmæa and as it treats all the important organs of the body except the shell, it would at first sight seem to render superfluous further work upon the small family of Acmæidæ. Various statements made by Haller have, however, been the object of vigorous criticism and in other particulars which

have not yet come under public discussion I have found myself unable to adopt his views or to confirm his observations. It is unfortunate that of Haller's four species three are incorrectly named (*cf.* Willcox, :00). One, *Scutellina galathea*, is in all probability an Acmæa but its specific name can only be surmised; for his two other Acmæas he employs the name Lottia, a synonym which was not only discarded by its author some sixty years ago but which has been since 1865 in use for another genus or subgenus, so that the Lottia of Haller is an entirely different animal from the Lottia of Carpenter and modern authors in general.

In 1898, appeared a brief monographic account by myself of *A. fragilis*. This paper dealing as it did entirely with preserved material which was studied almost exclusively by means of sections, left room for such completion and enlargement as is presented in the present work. In 1904, appeared an excellent paper on the anatomy of *Lottia gigantea* by W. R. Fisher to which I shall frequently have occasion to refer. The latest contribution is an article by Spillman in which (:05, pp. 553–564, 568–572) the heart and vessels of Acmæa are described.

Other papers which in the last decade have discussed the Acmæidæ have been occupied mainly with criticism of some of Haller's statements and with the presentation of counter observations. The chief matters in dispute have been the existence of a cœlom as distinct from the pericardial, nephridial, and gonadial cavities, the extent of the nephridium, the presence of a subradular organ. The chief disputants have been Haller, Pelseneer, Thiele, Willcox.

Methods

The first problem which faces any student of the Mollusca relates to narcotization. This is a much less important question among the limpets than in most other groups since the form of the body is such that no great amount of distortion can be effected even by the most powerful contraction. Proper extension of mantle and tentacles are the main results to be attained. For these purposes I have employed various methods — Epsom salts, cocaine, chloretone, stale sea water, fresh water. No one of these

methods was altogether successful. The cocaine — a 2% solution in 50% alcohol added drop by drop — produced extension of gill and cephalic tentacles. In specimens killed after this treatment, the subradular organ was likely to be extruded. Chloretone — crystals gradually added to sea water — produced at first a general extension but a larger dose brought about contraction. This agent is especially useful for narcotizing parts — as gills or tentacles — which it is desired to study while still alive. Extension of mantle tentacles is best obtained by killing in Gilson's fluid, extension of the mantle in general by this method or by allowing the animal to die in stale sea water, or, as recommended by Fisher, in fresh water.

The most satisfactory killing agents I have found to be picro-sulphuric acid, chrom-alcohol (equal parts of 70% alcohol and $\frac{1}{10}$% chromic acid), and corrosive sublimate with 5 to 20% of acetic acid. A weak — 5% — aqueous solution of sublimate preserves the external cilia better than a stronger one; this solution also I have employed with success for material in which it was desired to demonstrate mucus. The various osmic acid solutions — vom Rath's, Hermann's, Flemming's — have no marked superiority except for demonstrating certain glands as noted in the section on the integument. Picro-sulphuric acid has the advantage when used for very small specimens, of decalcifying the shell while leaving it *in situ*; in specimens killed in corrosive acetic the shell parts from the animal, in consequence I suppose of the pressure due to the more rapid evolution of gas brought about by the larger proportional amount of acid. An acid killing agent, as Bernard has pointed out, is desirable because it at once coagulates the mucus and thus renders the goblet cells more conspicuous.

For purposes of dissection it is desirable to have some specimens killed in formalin. The comparative transparency produced by this agent as well as its slight swelling action are often of advantage; it has the further good quality that it preserves at least for some time the color of the nephridial epithelium. A 2% solution is most satisfactory and it is of course desirable that the solution if acid should be neutralized. Opaque specimens for dissection are best killed in Gilson's fluid. It is perhaps unnecessary to add that details can often be made out better in specimens in which

the pressure on the viscera entailed by the contraction of the foot has been done away with either by removal of this organ or by slitting it lengthwise and thus opening the visceral cavity.

Sections were prepared by imbedding in paraffin, were stained usually with hæmalum and eosin or with Ranvier's picrocarmine and methylen blue, and were mounted in xylol balsam. For demonstration of mucus Mayer's mucicarmine was employed on sections of material killed in 5% sublimate solution. Endothelium was demonstrated by bathing the fresh membrane for half an hour in a mixture composed of four parts saturated aqueous solution of methylen blue and 96 parts $\frac{6}{10}$% salt solution, then leaving it for some hours in a saturated solution of ammonium picrate. Specimens thus prepared were mounted in glycerine saturated with ammonium picrate and have kept well for some years.

For macerations, good results have been obtained with Haller's fluid (*cf.* Lee's *Vademecum*, 4th ed., p. 318) and Bernard's fluid (Bernard, '90, p. 101).

Total preparations showing the innervation of thin structures like the mantle or the gill were most successful when stained with methylen blue and mounted in glycerine surcharged with ammonium picrate. Such preparations are fairly permanent.

Habits

Here should be intercalated the article on the biology of Acmæa already mentioned. To the facts there stated I have only to add that I have occasionally found in the nuchal cavities of specimens collected at Eastport tiny shells, measuring about one mm. in diameter which have been identified for me by Mr. Charles W. Johnson of Boston as in all probability the young of *Lacuna neritoidea* Gould. Whether these are commensals or merely accidental visitants I am not prepared to say.

The literature dealing with this section is incorporated in the list at the close of the present article. The statement by Dall that fertilization is internal was published not in 1879 but in 1882.

GENERAL DESCRIPTION

Acmæa testudinalis, like the limpets in general, has a somewhat dish-shaped shell, (Figs. 1 and 2), roughly conical in section and with a mouth (corresponding to the base of the cone) which is broadly oval though with the anterior part a trifle narrower than the posterior. The apex of the shell lies not over its center but about one third of the distance from the anterior end. It may be

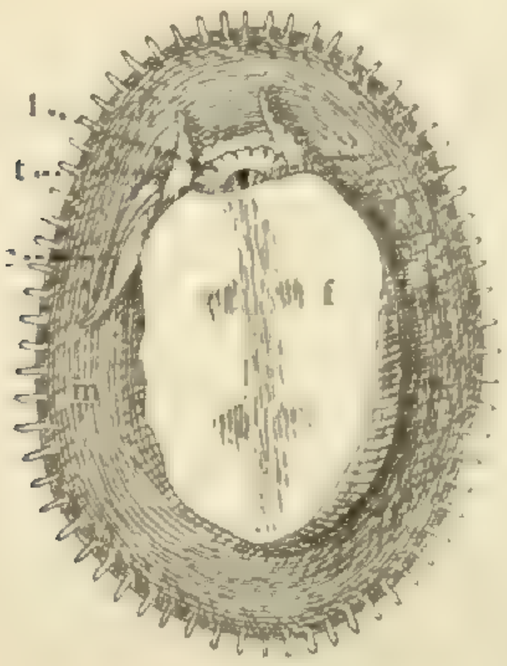

FIG. 1.

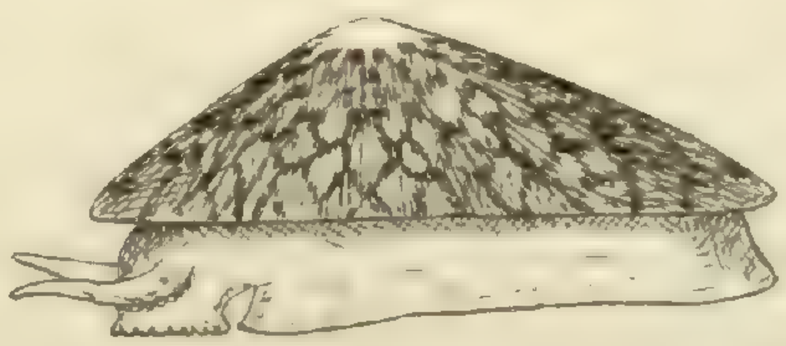

FIG. 2.

FIG. 1.— *Acmæa testudinalis*. Ventral view. × 1½. Whole animal with the exception of the mantle, strongly contracted. *c.*, ctenidium; *f.*, foot; *l.*, lip surrounding the circular mouth which is dilated to show the inner lips between which appears the dark radula; *m.*, mantle; *t.*, tentacle. Camera.

FIG. 2.— *Acmæa testudinalis*. Side view. × 1½. Camera.

worthy of mention that the true, or docoglossate limpets and the keyhole limpets (Fissurellidæ) differ in this respect from all the other widely dissimilar genera to which this form of shell is common and in which the apex, though varying in position in different forms, is never anterior. The condition in Acmæa is a secondary one for Boutan ('98, p. 1869) finds that in *A. virginea* the apex is at first posterior and only in course of development assumes the adult position.

In color the shell is usually yellowish gray marked with radiating stripes or tesselations of dark brown. The extent and the tint of the markings vary greatly and they are sometimes almost or quite absent. The hypostracum, or inner layer of the shell, stops a little short of its edge so that on the internal aspect the markings appear as a narrow border. This I understand to be the "more or less distinct internal border of the aperture," mentioned by Tryon and Pilsbry ('91, p. 5) as a character by which the Acmæidæ are

usually distinguished from the Patellidæ. While the family to which a limpet belongs may often be thus recognized, the genera at least of the Acmæidæ, cannot according to Pilsbry, be determined by a study of the shells alone.

In the living animal the mouth of the shell is almost entirely filled up by the foot, a broad fleshy expansion of the ventral body surface which apparently serves as a sucking disc[1] to hold the animal to the rocks on which it lives. The organ is composed chiefly of muscle fibers most of which run from the shell ventralward, spreading both laterally and toward the median line. A few fibers, however, are parallel with the sole and run either lengthwise or transversely. The fibers are imbedded in connective tissue and are entirely wanting near the margin of the foot, which is composed mainly of connective tissue excavated by large blood sinuses and is therefore extremely flexible. Certain marginal unicellular glands, whose secretion may aid the foot in clinging, are described, together with the epithelium in general, under the topic *Integument*. Just in front of the foot appears a ventral prolongation of the head, the muzzle; it bears on its tip the small circular mouth surrounded by the simple frill-like lip, which is characteristic of the subgenus Collisella. In a specimen which has been narcotized with chloretone the mouth is usually dilated enough to show the yellowish brown inner lips (Fig. 1) and in a fresh one its continual opening and closing permits a good view of the radula, which has a constant licking motion. It has been suggested by Davis and Fleure (:03, p. 49) that this movement serves to keep in motion the blood in the circumodontophoral sinus and thus reinforces the feeble ventricular muscles.

At the sides of the muzzle appear a pair of long and very contractile tentacles; they are borne on the posterior part of the head and each carries on the outer side of its base a simple optic pit which in the living animal or in a formalin specimen appears as a spot of black pigment.

In front of the head or at the right of the foot the ctenidium, or gill may usually be seen. When fully extended this organ is nearly

[1] This almost universally accepted view has been controverted by Davis ('95; Davis and Fleure, :03, pp. 4, 15) but the arguments do not seem to me conclusive.

one half as long as the entire animal; it is attached to the posterior wall of the nuchal cavity so that its distal end alone is visible (Fig. 3). It is a somewhat plume-like organ; the shaft of the feather is represented by a flattened triangular lamina, very long and very narrow, which bears on its flattened dorsal and ventral faces the structures corresponding to the barbs. These are two series of flattened more or less semicircular sacs each of which runs transversely across the shaft so that its cavity communicates with each of the two lateral vessels described below.

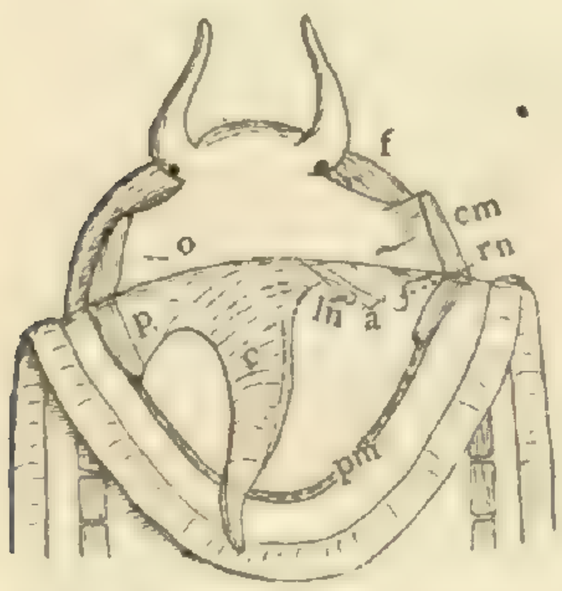

Fig. 3.— *Acmæa testudinalis.* Nuchal cavity. × 2. Columellar muscle cut and roof of chamber turned back. *a.*, anal papilla; *c.*, ctenidium; *cm.*, columellar muscle; *f.*, foot; *ln.*, *rn.*, left and right nephridial papillæ; *o.*, osphradium; *p.*, pericardium; *pm.* pallial muscle

Blood is conveyed through the gill by means of two vessels each of which occupies one margin of the shaft. That on the right edge conveys blood from the suprarenal plexus (*cf.* p. 184) to the gill, that on the left carries blood from the gill to the auricle. In the living animal the gill is usually so rotated that the efferent vessel alone is visible.

Attachment of the shell is effected by a band composed of the pallial and the columellar muscles (Fig. 4). The pallial muscle is ring-like and its fibers extend from the shell into the mantle. The columellar muscle is horseshoe-shaped and lies just internal to the pallial muscle from which it is separated by no sharp boundary; its fibers run from the shell into the foot and it is of course interrupted anteriorly where the head is interposed between these two structures.

From this muscle band depends the mantle, a thin, tentacle-fringed, membranous fold which lines the marginal part of the shell and in front of the columellar muscle runs up to the apex. In this region it forms the roof of a deep cavity, the nuchal cavity, which lies above the head and neck and is bounded at the sides and behind by the columellar muscle and the front part of the visceral mass. Elsewhere the mantle forms the outer wall of a groove-like space, the mantle groove, enclosed between it and the foot. Mantle groove and nuchal cavity are of course continuous; both together constitute the mantle cavity.

The dorsal part of the body is in the main developed into the convex visceral mass, but just above the anterior part of the foot it suddenly contracts into the neck (Fig. 2) and this, passing forward and slightly enlarging, gives rise to the head which curves ventralward and ends in the so called muzzle, thus bringing the mouth to lie flush with the foot. The head consists of a thin, muscular wall which in the region of the muzzle is fused with the pharyngeal walls but farther back is separated from them by a large blood sinus.

The visceral mass contains the digestive tract, blood vascular system, reproductive glands, and nephridia. It is covered by a green epithelium which immediately underlies the shell and may readily be brushed away. This being done, parts of all the above-mentioned organs may be made out through the thin body wall though they can be seen somewhat more readily in a specimen preserved in Gilson's fluid or formalin.

In such a preparation (Fig. 4) one notices first the band composed of pallial and columellar muscles; it is divided into a series of fascicles by blood vessels which cross it. External to the muscle ring is the mantle, fringed with its tiny tentacles and marked on the edge with a band of pigment whose alternations of light and dark tint have a general correspondence with the light and dark radial markings of the shell. In this region the mantle is thickened by the presence of a mass of unicellular glands of uncertain function. Just internal to the pigment band is a zone, often contracted to extreme narrowness, which represents the thin, non-glandular part of the mantle. Internal to the anterior curve of the pallial muscle and between the ends of the columellar muscle is a pellucid space, the roof of the nuchal cavity, in which may be noted traces of a blood plexus and through which the outlines of the ctenidium and the head may be more or less clearly seen.

Turning now to the visceral mass we note just internal to the columellar muscle and pericardium (see below) the edges of the generative gland; the bulk of the organ lies in the ventral part of the body directly above the foot, but its margins, especially the left one, curve dorsalward until they immediately underlie the nephridium through whose thin walls they are more or less clearly to be seen. Internal to the pericardium a small portion of the gland is

always distinctly visible. In the apical part of the visceral mass is the digestive gland; partly imbedded in it and partly lying between

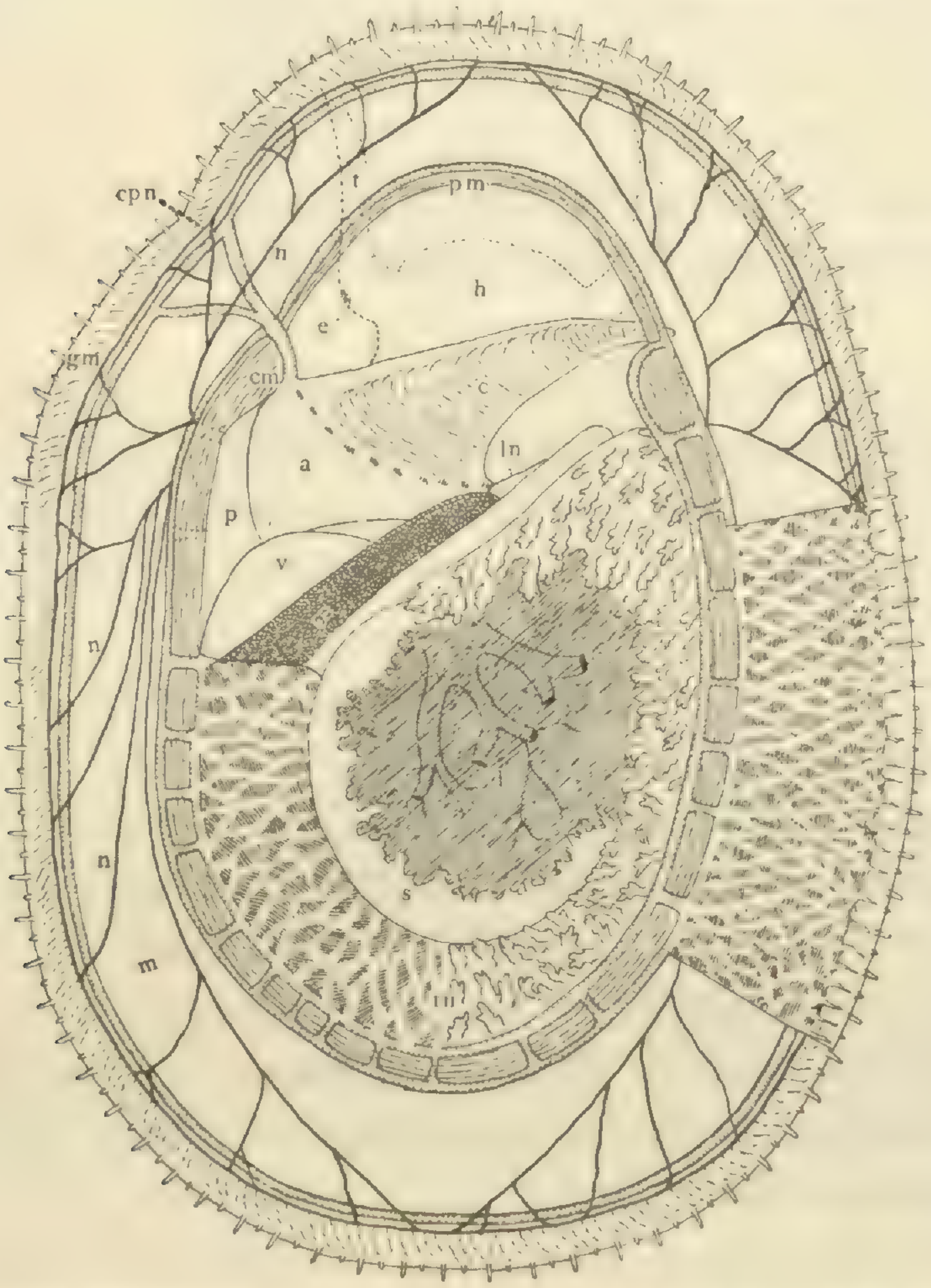

Fig. 4.— *Acmæa testudinalis*. Dorsal view with shell and superficial epithelium removed. × 4. *a*., auricle; *c*., ctenidium; *cm*., columellar muscle enclosing the nuchal cavity and visceral mass; *cpn*., circumpallial nerve ring, *d*., digestive gland; *e*., eye; *g*., generative gland; *gm*., glandular zone of mantle; *h*., head; *ln*., left nephridium; *n*., mantle nerve; *p*., pericardium; *rn*., right nephridium, its cœca on the right half of the figure represented in profile, on the left half represented *en face* thus giving the effect of a vascular plexus; *s*., stomach; *t*., cephalic tentacle; *v*., ventricle; the inner non-glandular portion of mantle is mostly represented as transparent but in a small section shows the vascular plexuses of which the ventral one underlies and obscures the external pallial vessel. The rectum, unmarked, lies between the generative gland and the right nephridium. For names of blood vessels see text. Two of the vertical interfascicular vessels are shown in dotted lines at the left; elsewhere they underlie and are obscured by the horizontal interfascicular vessels. Outlines drawn with camera, details combined from several specimens.

it and the generative gland are portions of the coiled alimentary tract especially the obliquely-running posterior end; sometimes a bit of the radula appears near the middle of the gland. On the left

side, abutting against the anterior portion of the columellar muscle is a pellucid triangular space, the pericardium. This space lies for the most part in the anterior, nearly vertical wall of the visceral sac and may in a preserved specimen of a ripe Acmæa be almost or quite hidden by the generative organ, which seems to overlie it. Such an appearance is, however, an artefact, being due to a folding of the anterior wall brought about by strong contraction. Behind the pericardium and abutting against the whole remaining extent of the columellar muscle lies the dorsal portion of the right nephridium; the ventral part of the organ occupies the right half of the ventral face of the visceral mass directly underlying the generative gland and is, of course, invisible from above. The marginal part of the dorsal nephridial wall is especially conspicuous for this is produced dorsally into numerous branched cœca that immediately underlie and are grown to the dorsal integument. Anteriorly the nephridium not only occupies the margin of the visceral sac but sends from its right limb toward the median line a large branched lobe which reaches and in part overlies the end of the intestine. On the left of the rectum between it and the pericardium, may be distinctly seen the small left nephridium, partly overlying the rectum.

The structures thus far described may, as has been stated, be made out more satisfactorily in a preserved specimen; the blood vessels now to be enumerated can be studied to much better advantage in a living animal though some of them are distinguishable in a preserved one. An Acmæa which has been kept in water of 15° to 25° C. until dead or dying is well relaxed. In such a specimen some at least of the mantle nerves may often be seen and it usually shows clearly the following vessels:—

1. Internal pallial vessel (*Mantelrandvene* or *Mantelrandarterie* of Haller), which lies just outside and beneath the pallial muscle and, like it, forms a complete ring.

2. Perivisceral vessel, a U-shaped vessel lying just inside the columellar muscle. On the right it is continued around the end of this muscle and across the pallial muscle to the internal pallial vessel; on the left it ends just behind the pericardium, where it falls into one of the horizontal interfascicular vessels.

3. External pallial vessel (pallial vein of authors), which forms

a second ring around the margin of the mantle at the base of the glandular zone.

4. The horizontal interfascicular vessels (*Quervenen* of Haller), a series of vessels which cross the columellar and pallial muscles connecting the perivisceral and the internal pallial trunks.

5. The vertical interfascicular vessels, a series of vessels which run up from the foot in the columellar muscle, join each with a horizontal interfascicular vessel and so connect with the internal pallial.

6. The mantle plexus. This consists of a dorsal and a ventral network. The vessels of the ventral network arise from the internal pallial trunk and the ultimate branches end blindly in the glandular zone. The vessels of the dorsal network arise from the external pallial trunk and end blindly in the non-glandular zone of the mantle. In a view such as we are describing the two networks are indistinguishable.

7. The transverse pallial vessels. One or two vessels, which arise from the external pallial trunk opposite the left end of the columellar muscle, unite (if two are present) and curve around the muscle to the auricle. In a relaxed specimen such as we are describing they cannot be traced to the auricle but in a perfectly fresh animal their pulsation is readily seen.

8. Indications of a suprarenal plexus (*periintestinales Venennetz* of Haller). The distal ends of the nephridial cœca are grown to the dorsal body wall and the blood sinus in which they lie is thus broken up into a series of connecting spaces.

9. Supravisceral vessels, which ramify over the dorsal surface of the digestive gland and open eventually into the suprarenal plexus. I have been most fortunate in finding these dorsal vessels showing clearly in specimens preserved in Gilson's fluid in which the contraction had been reduced to a minimum either by narcotizing with chloretone or by slitting the muscles of the foot.

10. Ctenidial vessels. In a preserved specimen one may see through the wall of the nuchal cavity the ctenidium with its dorsal series of lamellæ and the afferent and efferent vessels running respectively along its right (posterior) and left (anterior) edges. The afferent vessel brings blood from the suprarenal plexus, the efferent one carries it to the auricle. At the base of the gill may

be seen small opaque patches, the expression of interspaces between vessels that open directly into the auricle or the gill vessels. Those which open into the afferent vessel come from the anterior part of the suprarenal plexus; those which open into the auricle and the efferent vessel come from the nuchal plexus.

The nuchal cavity (Fig. 3), as has been said, lies in front of the visceral sac and above the head and neck; it is somewhat triangular in longisection and its posterior wall curves from side to side so that the cavity is much deeper from front to back in the median line than laterally. It contains the following structures, which with the exception of gill and pericardium are borne entirely on the posterior wall: pericardium with the enclosed heart, ctenidium, papillæ of small left and of large right nephridia, anal papilla. Separate generative openings are absent, as is also a hypobranchial gland.

On looking into the cavity from the front, one notices first the large ctenidium whose line of attachment runs along the mantle from the left tip of the columellar muscle obliquely back to the hinder wall of the cavity, where it ends a little on the right of the median plane. Through the thin posterior wall of the chamber can be seen the rectum lying near its dorsal edge and extending from the ctenidium almost to the right tip of the columellar muscle, where it ends upon a prominent anal papilla. Below the rectum appears a portion of the large right nephridium. It opens by a sizable papilla (infra-anal papilla of authors) located at the right of the anus. Above the rectum, in the triangle included between it, the gill, and the dorsal edge of the mantle cavity, lies the small left nephridium; it opens by an inconspicuous papilla (supra-anal papilla of authors) above and to the left of the anus. Behind and on the left of the ctenidium is a large triangular space enclosed between it and the columellar muscle and lying partly in the posterior and partly in the dorsal wall; this is the pericardium. The osphradia are so inconspicuous as to be readily overlooked; they are a pair of narrow transverse epithelial ridges which lie on the neck a little behind the anterior end of the columellar muscle. In a specimen whose shell was 35 mm. in length the left osphradium was 2 mm. long and the right 1.5 mm. According to Dall these structures are sometimes rendered conspicuous by an orange pigment; I have never seen such specimens.

Previous Investigations.—No extended account of the external anatomy of Acmæa has hitherto been published; the fullest description is embodied in a single paragraph by Forbes and Hanley ('53, p. 436). Haller's description of the mantle and gill will be discussed in subsequent sections.

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AFFINITIES OF CERTAIN CRETACEOUS PLANT REMAINS COMMONLY REFERRED TO THE GENERA DAMMARA AND BRACHYPHYLLUM[1]

ARTHUR HOLLICK AND EDWARD C. JEFFREY

Introduction

This paper is a preliminary contribution, designed to demonstrate the value of critical examinations of palæobotanical material by means of the microscope. The results obtained by such examinations of three kinds of Cretaceous fossil plant remains are described, *viz.*: cone scales commonly referred to the living genus Dammara, leafy branches commonly referred to the extinct Coniferous genus Brachyphyllum, whose exact botanical affinities have not heretofore been satisfactorily determined, and certain lignitic fragments found associated with the foregoing.

The first mentioned are shown to belong not to Dammara but to an extinct genus, closely related to it, to which the new generic name Protodammara is given. The second are shown to be Araucarinean in their affinities and probably to represent the branches of the tree which bore the cones from which the scales of Protodammara were derived. The third are shown to be referable to Araucarioxylon and probably to represent the wood of the tree which bore the leaves of Brachyphyllum and the cones of Protodammara.

[1] Read before the Botanical Society of America, New Orleans meeting, January 4, 1906.

Contributions from the Phanerogamic Laboratories of Harvard University. — No. 4.

Contributions from the New York Botanical Garden.— No. 79.

DISCOVERIES WHICH SUGGESTED THE PREPARATION OF THIS PAPER

The discoveries which suggested the preparation of this paper were described in a previous paper read before the Botanical Society of America at the Philadelphia meeting, on December 30th, 1904.[1] During the autumn of that year an interesting section of Cretaceous deposits was found exposed in the Androvette clay pit, at Kreischerville, Staten Island, N. Y. At this locality the deposits consist of irregularly stratified sands and clays, in one part of which occurs a lens-shaped bed of closely packed vegetable *débris*, consisting of leaves, cone scales, twigs, amber, charred wood, and lignite. At that time special attention was given to the amber and the other remains were merely examined superficially and briefly mentioned. The suggestion was made by Dr. Jeffrey that critical examination of the lignitic fragments would probably produce interesting results, and this suggestion led to two joint visits to Kreischerville during the past year and the collection of a large amount of new material, in part from the original locality and the remainder from the nearby Drummond pit. Some of the results obtained from the examination of this material form the basis of this contribution.

OBJECT AND SCOPE OF THE INVESTIGATION

One of the great difficulties in connection with any attempt to determine satisfactorily the relationships of palæobotanical specimens is due to the fact that such specimens are nearly always more or less fragmentary, being represented only by dismembered parts or organs of plants, and seldom or never by a complete individual organism. Under such conditions it is not surprising that descriptions based upon superficial characters only have frequently resulted in erroneous generic determinations; different parts of the same species have often been described under two or more specific or generic names; or occasionally a single specific

[1] Arthur Hollick. "The Occurrence and Origin of Amber in the Eastern United States." Published in *Amer. Nat.*, vol. 29, pp. 137–145, *pls. 1–3*, 1905.

name was made to include several different fragments which were subsequently ascertained to belong to two or more distinct species.

The identification or determination of a genus solely from the shape or superficial markings of a cone or some of its detached scales or of a leaf or a leafy twig, can seldom be entirely conclusive or satisfactory; but it may be readily appreciated that if, in addition, the internal structure of such specimens can be made out by the use of the microscope, not only may the genera be thus determined beyond question, but many fragmentary scattered remains, presenting no superficial characters of any diagnostic value, might thus be identified and brought together into their true generic and specific relationships.

Superficial examination of the Kreischerville material showed that it contained a number of recognized species, descriptions of which were based upon well defined external characters, besides quantities of specimens which were not identifiable by ordinary means. This indicated a specially favorable field for investigation, of which advantage was taken, and the methods employed, together with some of the selected results obtained, are here described.

Description of the Gross Material

Botanical Characters of the Plant Remains.— A rough examination of the gross material showed the presence of pteridophytes, angiosperms, and gymnosperms. The remains of the pteridophytes were exceedingly fragmentary and unsatisfactory. Those of the angiosperms consisted for the most part of dicotyledonous leaf impressions in the clay, usually accompanied by a thin film of carbonaceous matter, which generally disappeared on exposure to the air.

The remains of the gymnosperms proved to be more satisfactory, however, being represented not only by isolated coniferous leaves which retained more or less of the substance of the plant, but also by leafy twigs and branches, cones and cone scales, and fragments and logs of lignite, some of which contained amber in their interstices. Special attention was therefore given to these remains amongst which specimens of the following genera and species were separated out and identified.

List of the Coniferous Remains

1. Cone scales, allied to Dammara and similar to very small specimens of *D. microlepis* Heer. These are described in this paper on p. 199 under the new generic name Protodammara.

2. Cone scales and leaves of *Pinus* sp. The scales are relatively small. Several of the leaf specimens showed three in a bundle, enclosed in a sheath.

3. Leafy twigs of *Sequoia reichenbachi* (Gein.) Heer, *S. heterophylla* Vel., *Juniperus hypnoides* Heer, *Widdringtonites reichii* (Etts.) Heer, *Frenelopsis gracilis* Newb., and *Brachyphyllum macrocarpum* Newb.

4. Lignite and other fragmentary coniferous remains which could not be generically determined from their external characters.

5. Amber, occasionally in the interstices of the lignites, but for the most part in the form of small drops or "tears" and irregular fragments.

METHODS EMPLOYED IN THE CRITICAL EXAMINATION OF THE MATERIAL

Maceration and Separation of the Gross Material.—In the examination of the finer vegetable *débris* previously described the following method was employed. Caustic soda or potash in 1 to 3% solution was used with considerable success. After this treatment the fragments of plants were somewhat swollen and separated readily from one another and from the argillaceous matrix. The loosened clay was washed away on a wire gauze tray of not too fine meshwork and the lignitic or carbonaceous fragments were left in a clean and recognizable condition. The fragments in most cases were rather small, especially those of greatest interest, so that the most convenient method of recognition was by means of a dissecting microscope of very low magnification. A great many different kinds of coniferous remains were thus separated out and identified from their external appearance, as well as many charred specimens of dicotyledonous woods. Of these in general no account will be given at the present time, for attention was restricted to the cone scales similar to those referred by Heer to the genus Dammara, leafy branches belonging to the Brongniartian genus Brachyphyllum, and certain Araucarineous lignites. The chosen material was often in a very

good state of preservation especially when charred, or partially charred.

Sectioning and Microscopic Examination of Specimens.— In the case of lignitic or charred vegetable remains it is necessary for successful study to obtain very thin sections, on account of the dark color and opacity of the fossilized tissues. By the use of hydrofluoric acid for removing mineral matter and by embedding in thickened celloidin, it was found possible to make sections often of large area, as thin as 5 micra which proved admirable for photomicrographic purposes. These sections were cleared at once in benzole without previous staining, since the natural dark color of the lignites was sufficiently pronounced to differentiate the structures, even in very thin sections. In some cases it was found necessary to reduce the natural dark hue of the preparations and chlorine water was useful for this purpose. The sections were mounted in balsam on plate-glass slides and after previous drying were subjected to pressure and high temperature in the warm oven for the purpose of making them perfectly flat. All the photomicrographs in the present article were made by means of Zeiss lenses, except those showing surface features. The latter were executed with the admirable Heliar lenses of the Spencer Lens Co. Electric light was employed in all cases as the illuminant.

Descriptions of Specimens

Cone Scales Commonly Referred to Dammara. — Fossil cone scales similar to ours were described and figured for the first time by Professor Edward Hitchcock,[1] in his account of the organic remains found at Gay Head, Martha's Vineyard. They were not named by him, but his figures and description leave little to be desired. He says: "Figs. 4, and 5, represent different individuals of another variety of vegetable remains.... These are not mere impressions; but a scale of carbonaceous matter, mixed with amber, marks the spot where the vegetable was imprisoned....It seems to me very obvious that these remains must be the seed vessels of some coniferous plants."

[1] *Final Rept. Geol. Mass.*, vol. 2, p. 430, *pl. 19, figs. 4, 5*, 1841.

It was not until many years after Hitchcock's description was published that any further discovery of similar remains was made, or at least recorded, and to Professor Oswald Heer belongs the credit of first recognizing their affinities with the living Coniferous genus Dammara, in his description of specimens identical with those from Gay Head, under the name *D. borealis*,[1] from the Cretaceous of Greenland, in his discussion of which he says (p. 55): "Es haben diese Schuppen so grosse Aehnlichkeit mit derjenigen von Dammara (Agathis), dass wir sie derselben Gattung zutheilen dürfen." For purposes of comparison a figure of this species, representing a specimen collected at Gay Head, is shown on Plate 1, Fig. 1.

Two other so called species were also described and figured by the same author, *viz.*: *D. microlepis*[2] and *D. macrosperma*.[3] A specimen of the former, collected at the Gay Head locality, is shown on Plate 1, Fig. 2, which, by comparison, may be seen to differ from *D. borealis* merely in size. *D. macrosperma* has not been recognized in any collection of material except that from Greenland, and it is doubtful if it should be regarded as specifically distinct from the other two. In other words all three of these so called species might very well be included under *D. borealis*.

Heer was evidently in considerable doubt in regard to the identity of some of his specimens and also with regard to their botanical relationships. In his discussion of *D. microlepis* for example he says (p. 55, *loc. cit.*): "Hat einige Aehnlichkeit mit den Blüthenknospen des Eucalyptus Geinitzi," and a comparison with the figures of the objects which he refers to the fruit of that species[4] shows them to be so closely similar in appearance to his Dammara scales as to be practically indistinguishable from them.

Krasser, Beyer, and Velenovsky subsequently described and figured similar remains from the Cretaceous of Europe, with varying opinions as to their probable botanical affinities. The last

[1] *Fl. Foss. Arct.*, vol. 6, pt. 2, p. 54, *pl. 37, fig. 5*, 1882.
[2] *Ibid.*, p. 55, *pl. 40, fig. 5.*
[3] *Ibid.*, vol. 7, p. 17, *pl. 53, fig. 11*, 1883.
[4] *Ibid.*, vol. 6, pt. 2, p. 93, *pl. 45, figs. 4–9*, 1882.

author first referred them to *Eucalyptus geinitzi* Heer,[1] with the leaves of which species they were found closely associated, but later he called what are evidently identical remains *Dammara borealis* Heer.[2]

In 1889, Mr. David White visited Gay Head, and in the following year, in a paper "On Cretaceous Plants from Martha's Vineyard"[3] he described and figured specimens collected there, referring to them as follows (pp. 98, 99): "Next to the preceding species, the most numerous of the plants from Gay Head is *Eucalyptus Geinitzi* Hr., fig. 8–11, two of whose fruits, 'resembling unopened flowers of syngenesian plants,' were figured as 'scales of vegetable remains' in Hitchcock's Final Report. This species, first described from the Liriodendron beds (Middle Cretaceous) of Greenland, is abundant in and most characteristic of the Middle Cretaceous of Bohemia, and is also present in the same stage (Cenomanian) in Moravia. The specimen, fig. 11, is included here on account of its coincidence with one figured by Velenovsky (Foss. Flor. böhm. Kreide., iv, pl. xxv, fig. 7), which he supposed represented a flower of this species. It may belong to a conifer.

"The remains of the nuts show longitudinal furrows (white in the figures) filled with a resin which is 'indistinguishable by ordinary tests from Amber,' and which was observed and pronounced amber by Hitchcock in 1841. These doubtless are the remains of gum or oil vessels, such as exist in the nuts of recent Eucalypts; and the granules of 'amber' can hardly be else than Eucalyptus gum.

"The explanation is at once suggested that the fragments of amber observed by various writers, during the last hundred years, about Gay Head, and in the New Jersey Cretaceous, where also Eucalypts are found, are the product of the contemporaneous 'gum-trees,' rather than of some conifer. None of this American amber has, I believe, been tested for succinic acid, or to show its relation to true amber."

[1] *Foss. Fl. Böhm. Kreideform.*, pt. 4, p. 1 [62], *pl. 1* [*24*], *figs. 1, 2; pl. 2* [*25*], *figs. 6–11; pl. 4* [*27*], *fig. 13 in part*, 1885.

[2] *Kvet. Cesk. Cenomanu*, p. 7, *pl. 1, figs. 28, 29*, 1889.

[3] *Amer. Journ. Sci.*, vol. 39, p. 93–101, *pl. 2*, 1890.

At about this same time Dr. J. S. Newberry was engaged in the investigation of the Cretaceous flora of New Jersey, the results of which were later included in his "Flora of the Amboy Clays."[1] In this work he lists *Dammara borealis* Heer as a characteristic and abundant element of the flora, and says (pp. 46, 47): "In his Flora Fossilis Arctica (loc. cit.) Professor Heer describes and figures the scales of a conifer which very much resemble those of *Dammara australis*, and yet there are some reasons for doubting the accuracy of his reference. It may also be said that the fruit scales which he calls *Eucalyptus Geinitzi*....are without doubt generically the same.... the fruits figured by Heer under the name of Eucalyptus are plainly scales, and are parts of an imbricated cone. I say this with confidence, because it has happened that in the Amboy clays we have found numbers of them sometimes associated together, oftener scattered and showing both faces. A peculiarity of these scales is that they are striped longitudinally by clefts which are filled with an amber-like substance. This structure is plainly seen in those figured by Professor Heer on Pl. XLV. Similar scales are described in an article by Mr. David White on the fossil plants from Gay Head....

"The considerations which have led me to doubt whether these cone scales are those of Dammara are that we have found no Dammara-like leaves associated with them, whereas in New Jersey they occur in great numbers mingled with and sometimes apparently attached to the branchlets of an extremely delicate conifer much like Heer's *Juniperus macilenta*.... Almost no other plant except this conifer is found with the cone scales, and it is difficult to avoid the conclusion that they belong together. Another reason for doubting whether these are the scales of a Dammara is that in some of them traces of two seeds are apparently visible, while in Dammara there is but one seed under each scale."[2]

The discussion is further continued by Dr. Newberry under his

[1] *Monogr. U. S. Geol. Surv.*, vol. 26, 1895.

[2] This observation by Dr. Newberry is particularly interesting in the light of what we now know in regard to the Kreischerville specimens, as may be appreciated by referring to our description of the seed scars on those scales, on p. 199.

description of *Juniperus macilenta*, on pp. 54, 55 (*loc. cit.*), as follows: "Thickly scattered among the twigs there are cone scales and cones .... The cone scales are evidently identical with those described by Heer under the name of *Dammara microlepis*.... and probably with those described by him as *Dammara borealis*." He says, however, that they cannot belong either to *Dammara* or to *Juniperus* and finally concludes with the hope "that in the future material will be obtained that will enable us to reconstruct this tree and determine with accuracy its botanical relations."

Dr. Newberry again refers to the scales in connection with his discussion of *Eucalyptus? angustifolia*, in the following words (*ibid.*, p. 111): "Professor Heer feels strengthened in his reference of leaves having this nervation to Eucalyptus by finding in company with them what he regards as the fruit of Eucalyptus; but in my judgment the examples he gives of this fruit....are rather detached scales of the cone of some conifer, and probably generically identical with the cone scales which he has called *Dammara borealis*."

Some years ago the senior writer of this.paper began an investigation of the Cretaceous flora of the Atlantic coastal plain, and in the material collected in New Jersey and on Staten Island, Long Island, Block Island, and Martha's Vineyard, numerous specimens of cone scales were found, some of them unquestionably identical with *Dammara borealis* or *D. microlepis* as defined by Heer, and others which apparently represented new species. Following are references to the specimens in question:—

"*Dammara borealis*, Heer?" Tottenville, Staten Island. *Trans. N. Y. Acad. Sci.*, vol. 12, p. 31, *pl. 1, fig. 17*, 1892.

"*Dammara borealis*, Heer." Chappaquidick, Martha's Vineyard. *Bull. N. Y. Bot. Gard.*, vol. 2, p. 402, *pl. 41, fig. 6*, 1902.

"*Dammara microlepis* Heer (?)." Ball's Point, Block Island. *Ann. N. Y. Acad. Sci.*, vol. 11, p. 57, *pl. 3, figs. 9 a, b*, 1898. At the time when these two specimens were described they were only referred provisionally to this species, in the following words: "The ones under consideration are, however, smaller than any which have been previously figured and might perhaps be referred to a new species, but in view of the limited amount of material and its fragmentary condition, I have thought it best to refer the speci-

mens provisionally to Heer's species." I am now satisfied that they belong to the new genus and species hereafter described and they are included, for comparison, on Plate 1, Figs. 12, 13.

"*Dammara Northportensis* sp. nov." Little Neck, Northport Harbor, Long Island. *Bull. N. Y. Bot. Gard.*, vol. 3, p. 405, *pl. 70, figs. 1, 2*, 1904. A figure of this species is reproduced on Plate 1, Fig. 4.

"*Dammara* (?) *Cliffwoodensis* n. sp." Cliffwood, N. J. *Trans. N. Y. Acad. Sci.*, vol. 16, p. 128, *pl. 11, figs. 5–8*, 1897. A figure of the type specimen of this species is reproduced on Plate 1, Fig. 3. This species may also be found described and figured by Mr. Edward W. Berry in his "Flora of the Matawan Formation (Crosswick's Clays)," [1] and again in a subsequent paper on "Additions to the Flora of the Matawan Formation"; [2] but the figures more nearly resemble *D. borealis* than they do the species to which they are referred, and the author himself remarks, in regard to the one last mentioned (p. 70): "The specimen is an unusually perfect one.... In outline and size it is very similar to the scale from Tottenville referred by Hollick to *Dammara borealis* Heer."

Finally may be mentioned the species described and figured by Dr. F. H. Knowlton, under the name *Dammara acicularis*, in his "Fossil Plants of the Judith River Beds," [3] which differs from all the other species in the possession of a well defined apical awn or spine, although in many of our individual specimens a similar feature, of smaller size, is present, and in others its former presence is clearly indicated.

If all the opinions expressed by the authors in the papers quoted, are analyzed it may be seen that a majority favor the idea that the scales are Coniferous and that their relationships are with *Dammara*, or with some other genus closely allied to it. Whether more than one species is represented in the various forms that have been described as such is a problem which yet remains to be solved and its solution will doubtless be attended with more or less difficulty, but the identification of the genus to which each form belongs should be a comparatively easy task, provided the

[1] *Bull. N. Y. Bot. Gard.*, vol. 3, p. 61, *pl. 48, figs. 8–11*, 1903.
[2] *Bull. Torrey Bot. Club*, vol. 31, p. 69, *pl. 1, fig. 11*, 1904.
[3] *Bull. U. S. Geol. Surv.*, no. 257, p. 134, *pl. 15, figs. 2–5*, 1905.

material available for study is such that it can be sectioned and subjected to critical examination under the microscope. Thus far the only specimens which we have so examined are those from Kreischerville, but it is hoped that the investigation may be continued in the future so as to include specimens from other localities.

Protodammara speciosa n. gen. et sp.

Plate 1, Figs. 5–13; Plate 2, Figs. 1–5

"*Dammara microlepis* Heer (?)." Hollick, *Ann. N. Y. Acad. Sci.*, vol. 11, p. 57, *pl.* 3, *figs.* 9 *a*, *b*, 1898.

Organisms consisting of kite-shaped cone scales, from 4 to 6 mm. long by 4 to 6 mm. broad above, abruptly narrowed from about the middle to the base, rounded, incurved, and apiculate above; resin ducts five or more, extending down the lower surface of the limb; seed scars three in number, crescentically arranged above the middle and approximately in the broadest part of the scale, with the central one higher up than the laterals.

Plate 1, Figs. 5–13, shows the scales natural size; Plate 2, Figs. 1 a, b, c, 2, shows four specimens with the upper surfaces exposed, magnified about ten diameters. Although they may be seen to resemble closely those of a small female cone of Dammara they are distinguished from the scales of that genus by the apical process and by the fact that they obviously bore three seeds instead of only one. It might indeed be inferred, from the presence of three apically attached ovules, that we have here to do with cone scales of one of the Sequoiineæ, rather than with one of the Araucarineæ, but the internal structure shows that they are truly Araucarian.

Plate 2, Fig. 3, represents a transverse section of the base of a scale, magnified about 40 times. A little below the middle point may be seen a single small fibrovascular bundle. At a higher plane of section this separates off a single upper bundle of inverted orientation and gives off a number of lateral bundles to the lower surface of the scale. The upper bundle supplies the seeds. In the higher part of the scale the inferior bundles are surrounded

by a dense cordon of transfusion tissue. The arrangement of the bundles of the scale presents throughout a close resemblance to that found in Dammara.

Plate 2, Fig. 4, represents about half of a transverse section of a scale, magnified about 50 times. The funicular attachment of one of the lateral seeds may be seen on the upper surface of the scale.

Plate 2, Fig. 5, shows a longitudinal section through the apex of the scale, which at the same time is also nearly median, magnified about 40 times.

There can be no doubt that these scales are Araucarian and that while they resemble the genus Dammara they do not belong to it. We have therefore proposed for them the generic appellation Protodammara.

Formation and Locality: Cretaceous clays, Raritan Formation. Pl. 1, Figs. 5–11 and Pl. 2, Figs. 1 a, b, c, 2, Kreischerville, Staten Island, N. Y.; Pl. 1, Figs. 12, 13, Ball's Point, Block Island, R. I.

Leafy Branches Commonly Referred to Brachyphyllum.—This genus was based upon the external characters of certain leafy branches, of Jurassic age, and was described under the noncommittal heading "Conifère douteuse." The type of the genus is *B. mamillare* Brongt., which he described but did not figure.[1] The species was figured by subsequent authorities however, notably by Saporta,[2] one of whose illustrations (fig. 4, *loc. cit.*), is reproduced on Plate 1, Fig. 14. A number of other species have also been described under the genus and under the closely related or synonymous genera Echinostrobus, Arthrotaxites, Thuites, Palæocyparis, etc. By some authors these genera have been all included under Brachyphyllum and by others they have either been regarded as distinct or else they have been grouped in various combinations. Their true botanical relationships, however, were never satisfactorily determined, although they were generally considered as allied to the Sequoiineæ or the Cupressineæ and as related to Arthrotaxis, Thuja, or Glyptostrobus. The species

[1] *Prod. Hist. Veg. Foss.*, p. 109, 1828.
[2] *Plantes Jurassiques*, vol. 3, *pl. 34, figs. 3–7*, 1884.

described by the earlier authors were all from Jurassic horizons but subsequently species were described from the Cretaceous,[1] and it is with these that we are especially concerned.

The question of generic identity between the several allied forms does not, however, come within the scope of this paper. The only matter which is of immediate concern is the fact that we have found at Kreischerville the leafy branches of a Brachyphyllum and have been able to determine, for the first time, by means of its internal structure, the exact relationship which it bears to certain living Coniferæ. This species is the same so far as external characters are concerned, as that described by Newberry from the Amboy clays of New Jersey (*B. macrocarpum* Newb., *loc. cit.*), and it has also been found at Northport, Long Island, and at Cliffwood, N. J. A reproduction of Newberry's fig. 1 (*loc. cit.*) is shown on Plate 1, Fig. 15, and the Northport specimens on the same plate, Figs. 16, 17. These are all natural size.

Plate 3, Figs. 1 a, b, c, shows three fragments of branches from Kreischerville, magnified about 6 times, and Fig. 2, on the same plate, shows one magnified about 10 times.

Plate 3, Fig. 3, shows a piece of another branch magnified about the same as the latter, and illustrates particularly well the longitudinal converging striæ characteristic of the leaves of Brachyphyllum.

Plate 3, Fig. 4, represents a transverse section through a relatively old branch, magnified by 8, in which the woody cylinder is well developed. The pith has largely collapsed, although it consists in large part of sclerotic cells.

Plate 3, Fig. 5, shows a transverse section of a young branch, magnified by 15. Four leaves may be seen on the margins of the figure, and of these, those on the broad upper and lower surfaces of the branch overlap those on the margins, as they are cut through at a higher region. The leaves are attached to the surface of the stem by practically all of their ventral surface, with only a very

[1] *Echinostrobus squamosus* Vel., *Gymnosp. Böhm. Kreideform.*, p. 16. *pl. 6, figs. 3, 6–8*, 1885; *Thuites crassus* Lesq., *Cret. and Tert. Fl.*, p. 32. 1883; *Brachyphyllum macrocarpum* Newb., "Fl. Amboy Clays" (*Monogr. U. S. Geol. Surv.*, vol. 26), p. 51, footnote, *pl. 7, figs. 1, 2, 5, 7*, 1895.

narrow border left free, where in their upper portions they overlap their neighbors. The anatomical features cannot be made out in this section as the magnification is not sufficient.

Plate 4, Fig. 1, shows a transverse section through the woody cylinder of the younger branch shown on Plate 3, Fig. 5. By using a lens it may be seen that at this stage the cylinder consists of clearly separated bundles. On the right a single leaf-trace is passing off.

Plate 4, Fig. 2, reproduces a cross section of the basal portion of a leaf from the margin of the same young branch. It may be seen that there are several fibrovascular bundles present. These have originated from the single trace previously described. Of the Cupressineæ, Sequoiineæ, and Araucarineæ, the only Conifers with which Brachyphyllum has ever been placed, *the latter group alone have the branched leaf-trace.*

Plate 4, Fig. 3, shows a similarly branching leaf-trace from one of the broad leaves which clothe the upper and lower surfaces of the stem in the genus Brachyphyllum.

Plate 4, Fig. 4, shows a portion of the latter under a higher degree of magnification. The lower fibrovascular tissue is obviously dividing into three branches.

Plate 4, Fig. 5, is part of a branch of Brachyphyllum in transverse section. The light spaces are the sections of resin-canals. Although the material was passed through a number of solvents of resin, used in a hot condition, there is still some matter present in the lumina of the resin-passages. This appears to be of a mucilaginous nature *and is comparable to that found among living Conifers only in the genera Araucaria and Dammara.*

Plate 4, Fig. 6, shows a transverse section of a diseased branch of Brachyphyllum, in which there is one particularly large resin-cavity. The fossil mucilage, as we consider it to be, is present also in this instance. We have, in fact, found this substance to be always present in Brachyphyllum, except in charred branches, and those which had become very rotten in the process of fossilization. *The mucilaginous contents of the resin-canals afford another reason for associating Brachyphyllum with the Araucarineæ rather than with the Cupressineæ or the Sequoiineæ.*

The most important argument, however, in favor of the Arau-

carineous nature of Brachyphyllum is the structure of the wood and phloëm. Plate 5, Fig. 1, is a longitudinal radial section of the tracheids of the wood, highly magnified. *They show the flattened and alternating bordered pits, which are the diagnostic feature of Araucarioxylon Kraus.*

Plate 5, Fig. 2, makes the diagnosis beyond dispute, as *it shows the very striking Araucarineous character of the rays.* Plate 5, Fig. 3, represents a transverse section through the xylem and phloëm in a yearling branch. Plate 5, Fig. 4, shows two bundles in the young stem of Brachyphyllum. It may be seen that *the region of the phloëm is marked by the absence of the regularly alternating rows of hard bast-fibers, which are found without exception in the phloëm of all Cupressineous and Sequoiineous Conifers.*

Lignites Referable to Araucarioxylon.— Associated with the cone scales of Protodammara and with the leafy branches of Brachyphyllum are found numerous specimens of lignite, amongst which are two types of Araucarioxylon. The first of these is very similar to the wood of the living Dammara, and like Dammara it is characterized by the presence of resinous tracheids. The pith, when present, is seen to be large and composed mainly of tanniferous cells as in that genus. When wounded the wood of this Araucarioxylon does not give rise to traumatic resin-canals.

The second type, so far as we have been able to observe, does not possess resinous tracheids. The pith, when present, is sclerified and of small size as in Brachyphyllum. The wood, when injured, forms resin-canals of a traumatic character.

Plate 5, Fig. 5, shows a row of traumatic resin-canals in this species. Plate 5, Fig. 6, shows one of these resin-canals and the adjacent wood, highly magnified. The tracheids of the wood are seen to be free from resin. *This type of Araucarioxylon appears to be the wood of Brachyphyllum,* while the type first described appears to belong to Araucarian Conifers more nearly allied in structure to those now in existence.

CONCLUSIONS

The cone-scales referred by Heer to Dammara, at least in the case of those from Kreischerville, do not belong to that genus but to the hitherto unrecognized Araucarinean genus Protodammara.

The leafy shoots and branches from several eastern American Cretaceous beds referred by various authors to Brachyphyllum[1] are of Araucarian affinities, as shown by their structure and as indicated by their constant association with the cone scales of Protodammara.

A large part of the lignites associated with both the above are Araucarineous and probably represent in part the wood of the trees which bore the leafy branches of Brachyphyllum and the cones of Protodammara.

The latter genus was in all probability the last survivor of an ancient Araucarian line of descent, joined near its base with the primitive stocks of the Abietineous and Cupressineous series. Its anatomical characters show that it was forced to occupy less advantageous situations in Cretaceous times, and possibly in earlier periods as well. It may have grown on dry hills, while the better adapted related forms, which still survive in the modern genera Araucaria and Dammara, flourished in the richer lowlands, in company with other gymnosperms of higher type of development and with the angiosperms, which even then had begun to assume the predominant position which they occupy to-day.

[1] We do not consider it by any means proved, that all the leafy branches of the type of Brachyphyllum are necessarily Araucarian. It appears not improbable that some of the shoots of this general type may belong to other families of the Conifers. This for example may well be the case with some Coniferous remains recently described by M. Zeiller, from the upper Lias of Madagascar and referred to Sequoiineous affinities. In this instance the cones were found attached to the branches and the author remarks that the superior portion of the cone scale terminates "en une pointe obtusement aigue", a somewhat suspicious feature of resemblance to our Protodammara.

PLATE 1

FIG. 1.— *Dammara borealis* Heer, natural size. Gay Head, Martha's Vineyard, Mass.

FIG. 2.— *Dammara microlepis* Heer, natural size. Gay Head, Martha's Vineyard, Mass.

FIG. 3.— *Dammara cliffwoodensis* Hollick, natural size. Cliffwood, N. J.

FIG. 4.— *Dammara northportensis* Hollick, natural size. Little Neck, Northport Harbor, Long Island, N. Y.

FIGS. 5–13.— *Protodammara speciosa* n. gen. et sp., natural size. Figs. 5–11, Kreischerville, Staten Island, N. Y.; Figs. 12, 13, Ball's Point, Block Island, R. I.

FIG. 14.— *Brachyphyllum mamillare* Brongt. (after Saporta), natural size.

FIG. 15.— *Brachyphyllum macrocarpum* Newb., natural size. South Amboy, N. J.

FIGS. 16, 17.— *Brachyphyllum macrocarpum* Newb., natural size. Little Neck, Northport Harbor, Long Island, N. Y.

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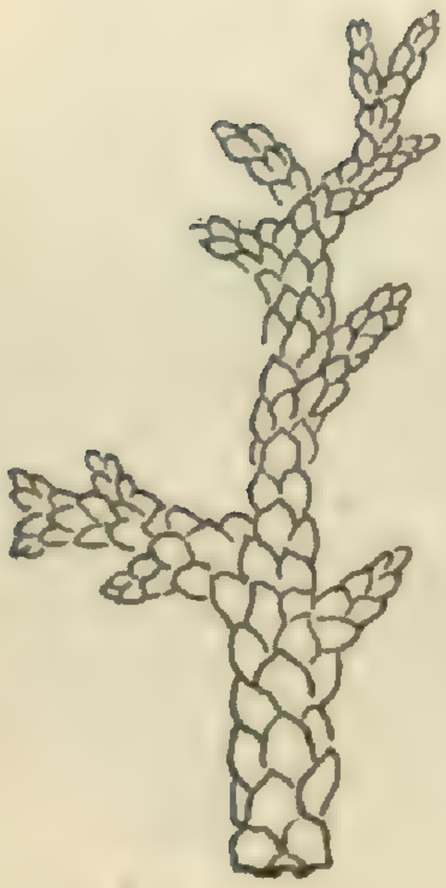

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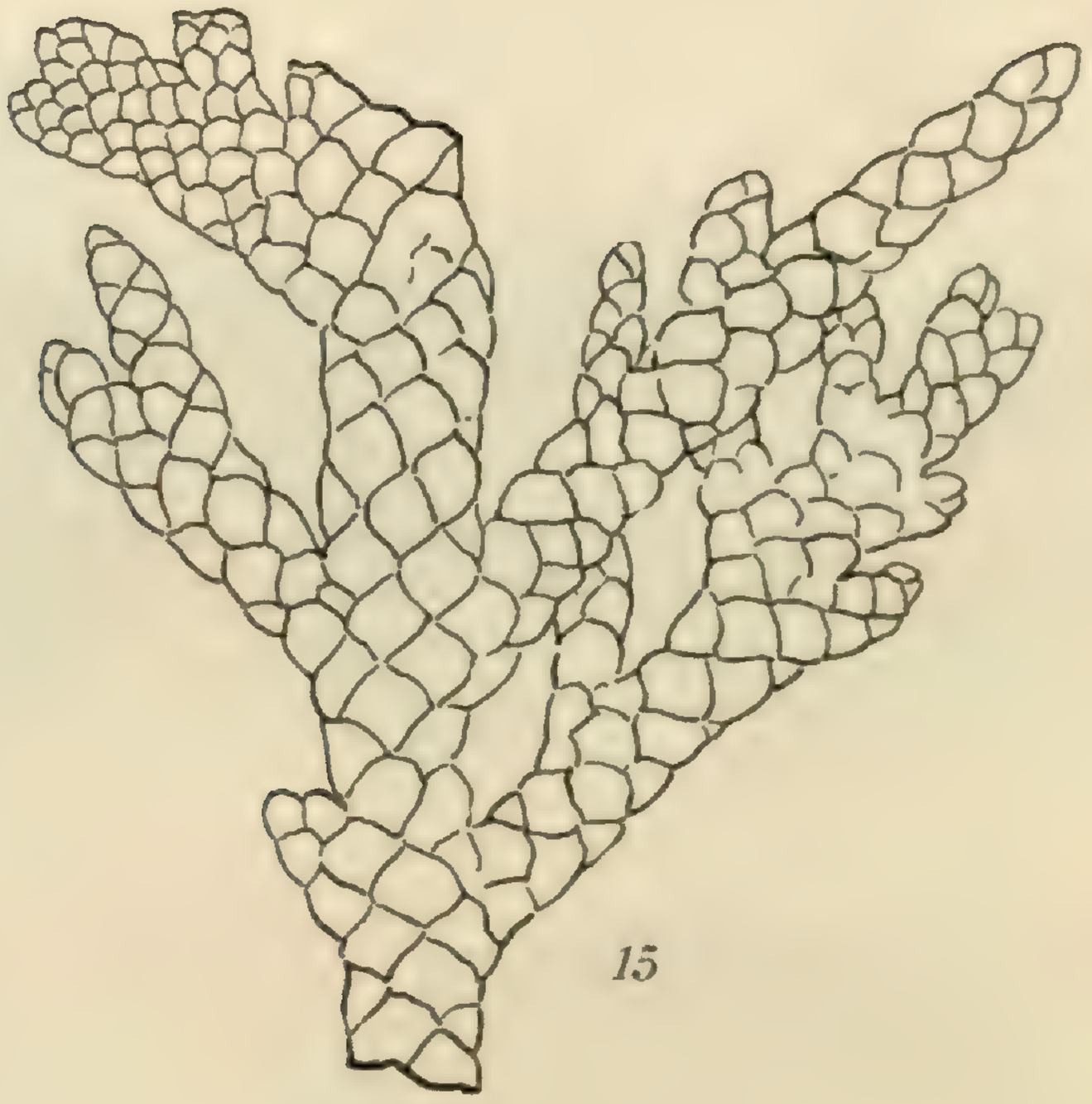

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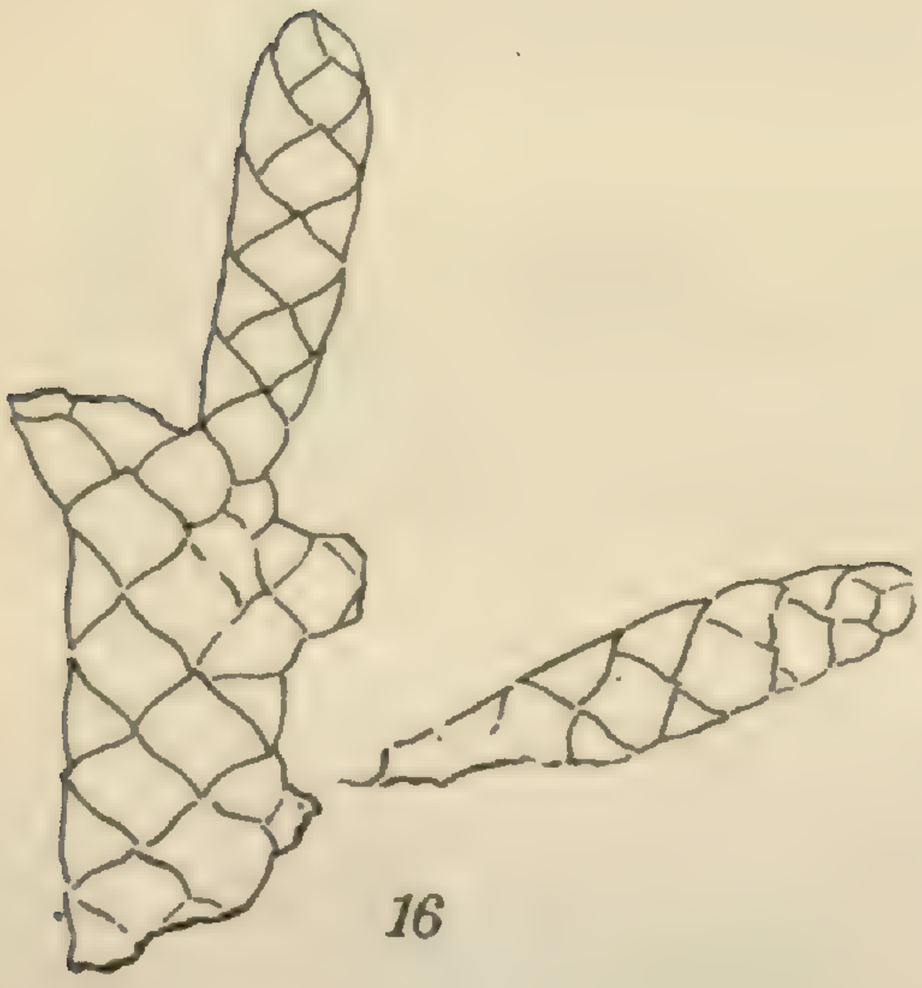

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PLATE 2

Figs. 1–5.— *Protodammara speciosa* n. gen. et sp., enlarged. Kreischerville, Staten Island, N. Y.
Figs. 1 a, b, c, 2.— Upper surface of cone scales, × 10, or more.
Fig. 3.— Transverse section of the base of a scale, × about 40.
Fig. 4.— About half of a transverse section of a scale, × 50.
Fig. 5.— Longitudinal section through the apex of a scale, × 40.

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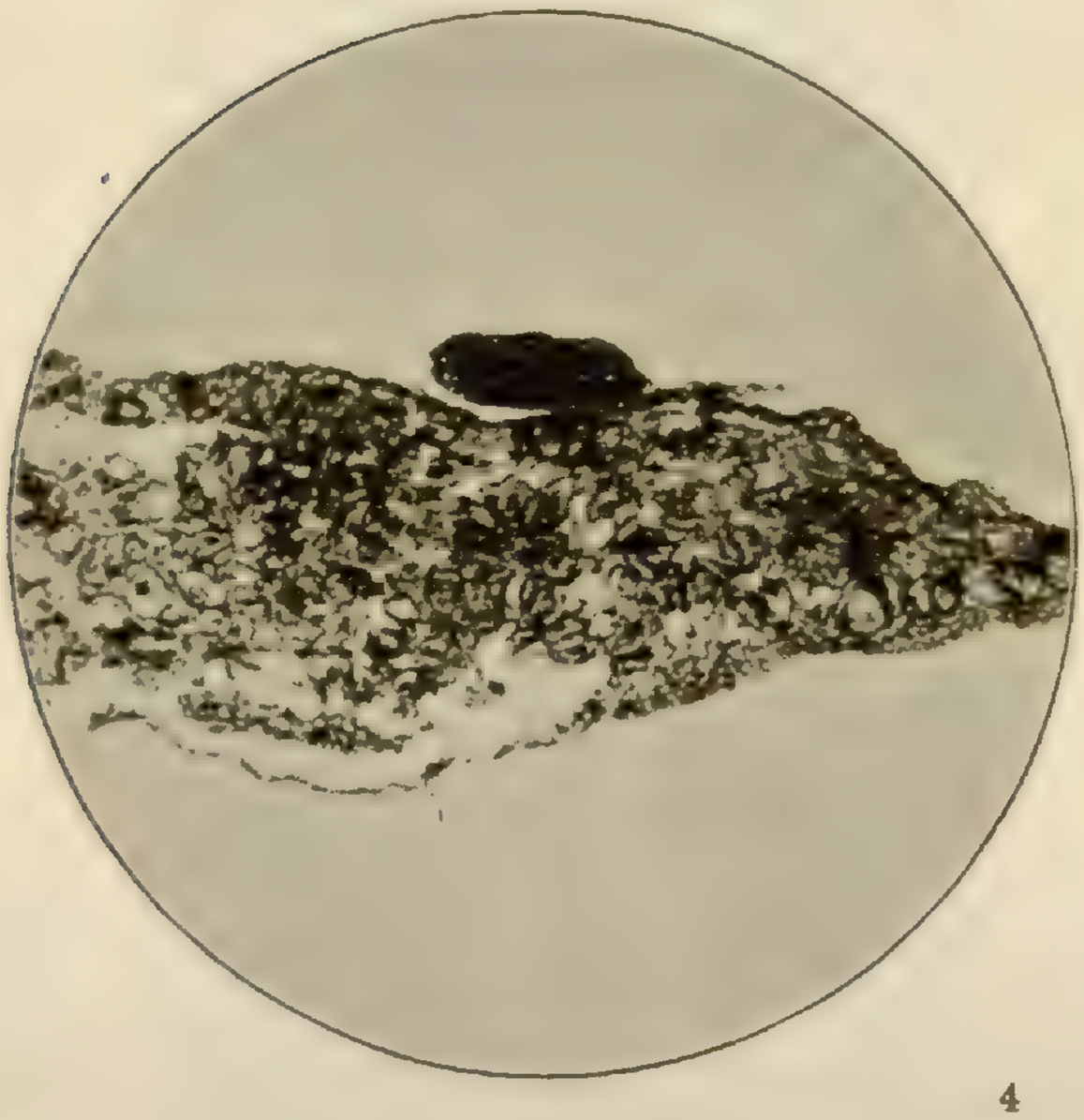

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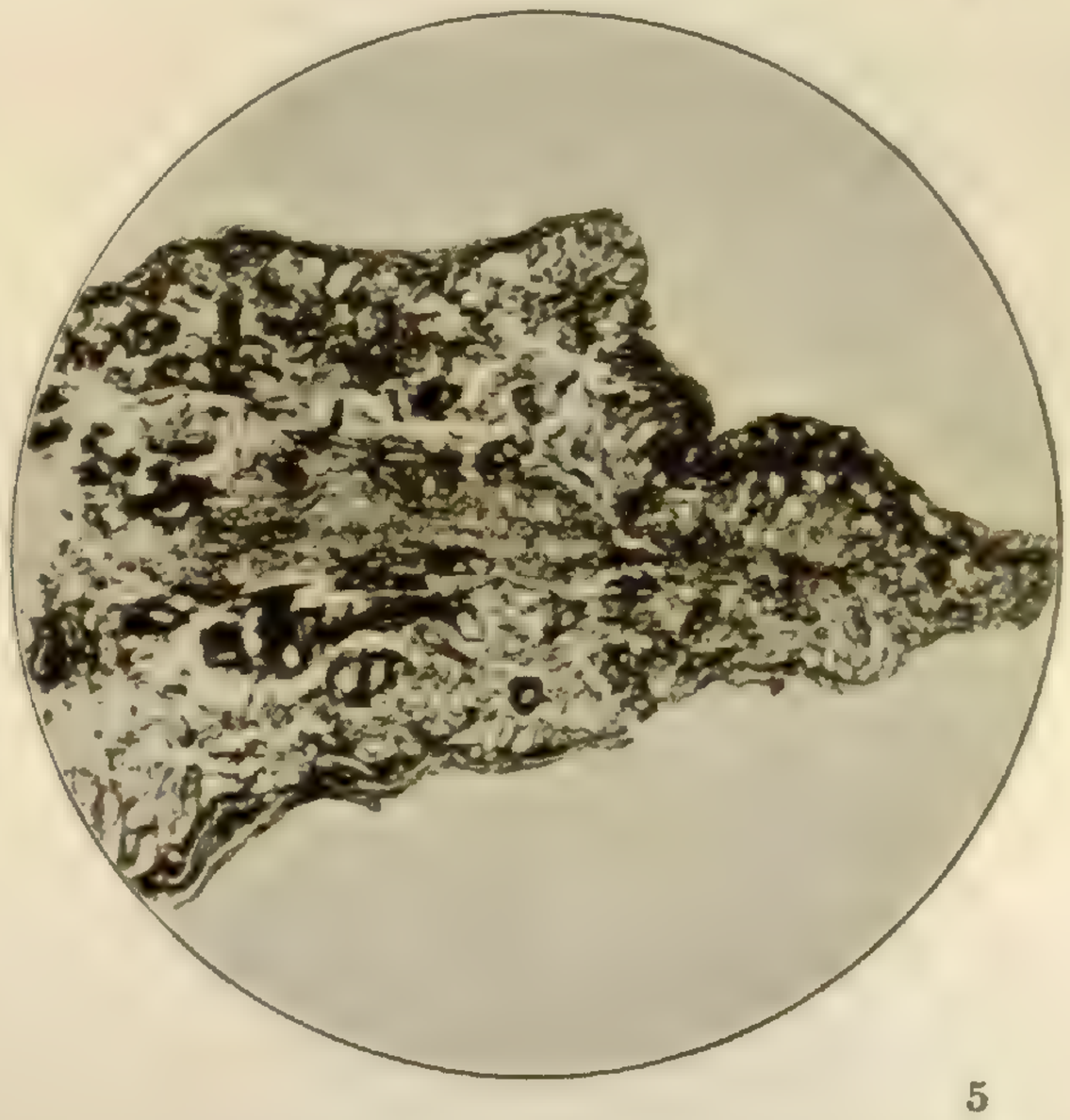

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PLATE 3

FIGS. 1–5.— *Brachyphyllum macrocarpum* Newb., enlarged. Kreischerville, Staten Island, N. Y.
Figs. 1 a, b, c. — × about 6.
Figs. 2, 3.— × about 10.
Fig. 4.— Transverse section through a relatively old branch, × 8.
Fig. 5.— Transverse section through a young branch, × 15.

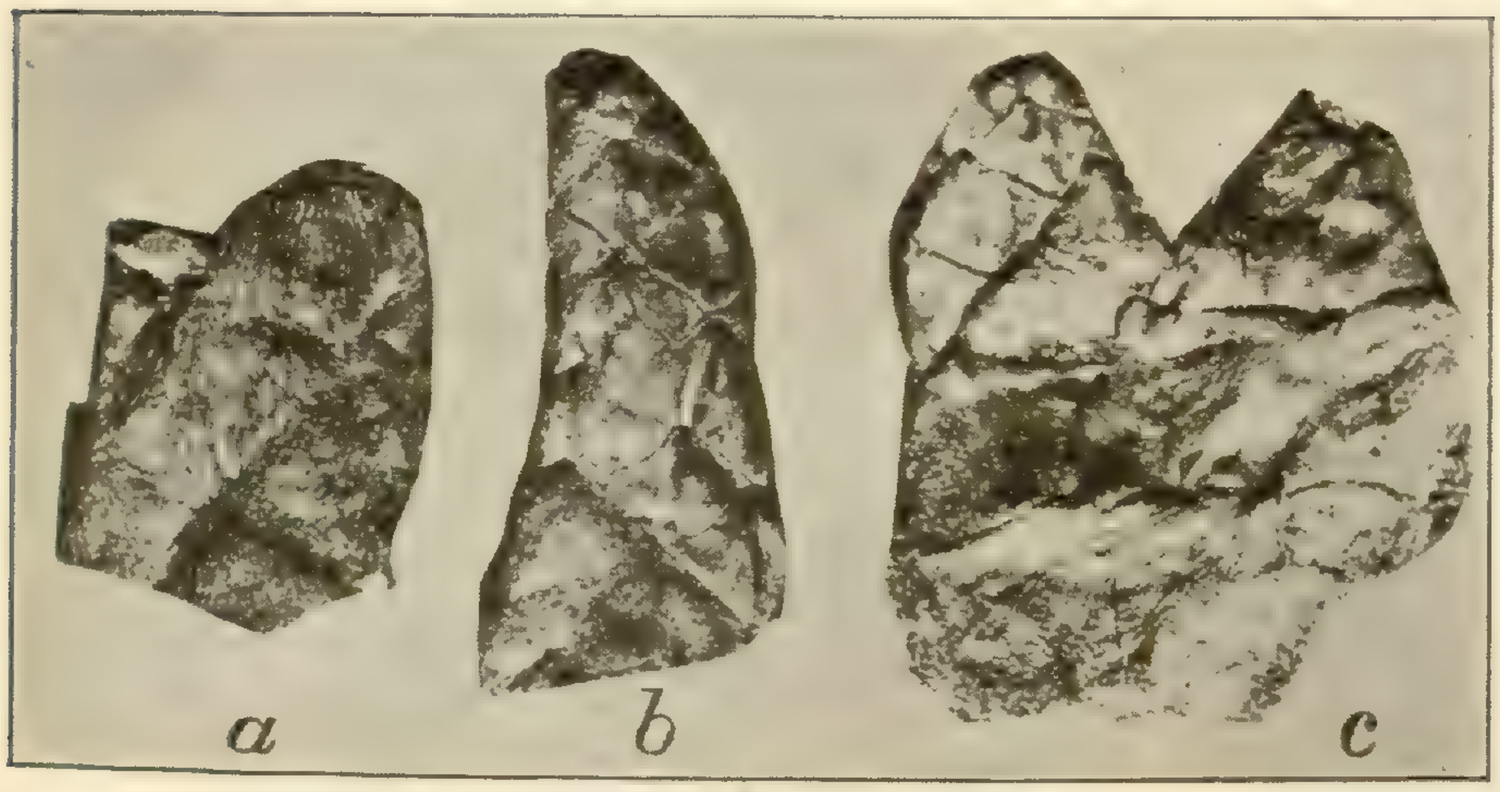

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PLATE 4

FIGS. 1–6.— *Brachyphyllum macrocarpum* Newb. enlarged. Kreischerville, Staten Island, N. Y.

Fig. 1.— Transverse section through the young woody cylinder of the branch shown on Plate 3, Fig. 5.

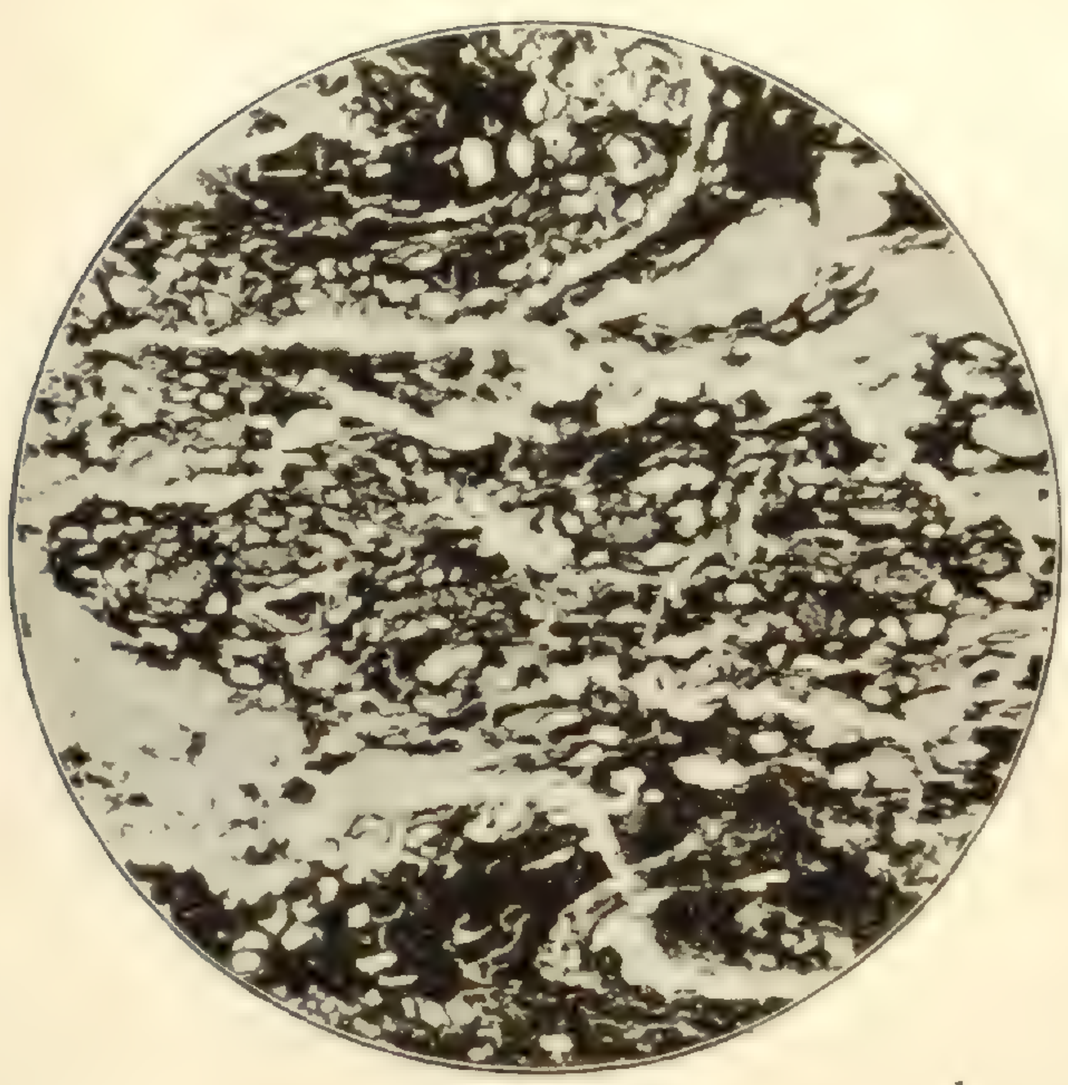
Fig. 2.— Cross section of the basal portion of a leaf from the margin of the same, × 50.

Fig. 3.— Same, showing a branching leaf trace, × 50.

Fig. 4.— More highly magnified, × 70.

Fig. 5.— Transverse section of a branch, showing resin-canals, × 30.

Fig. 6.— Transverse section of a diseased branch, showing a particularly large resin-canal, × 30.



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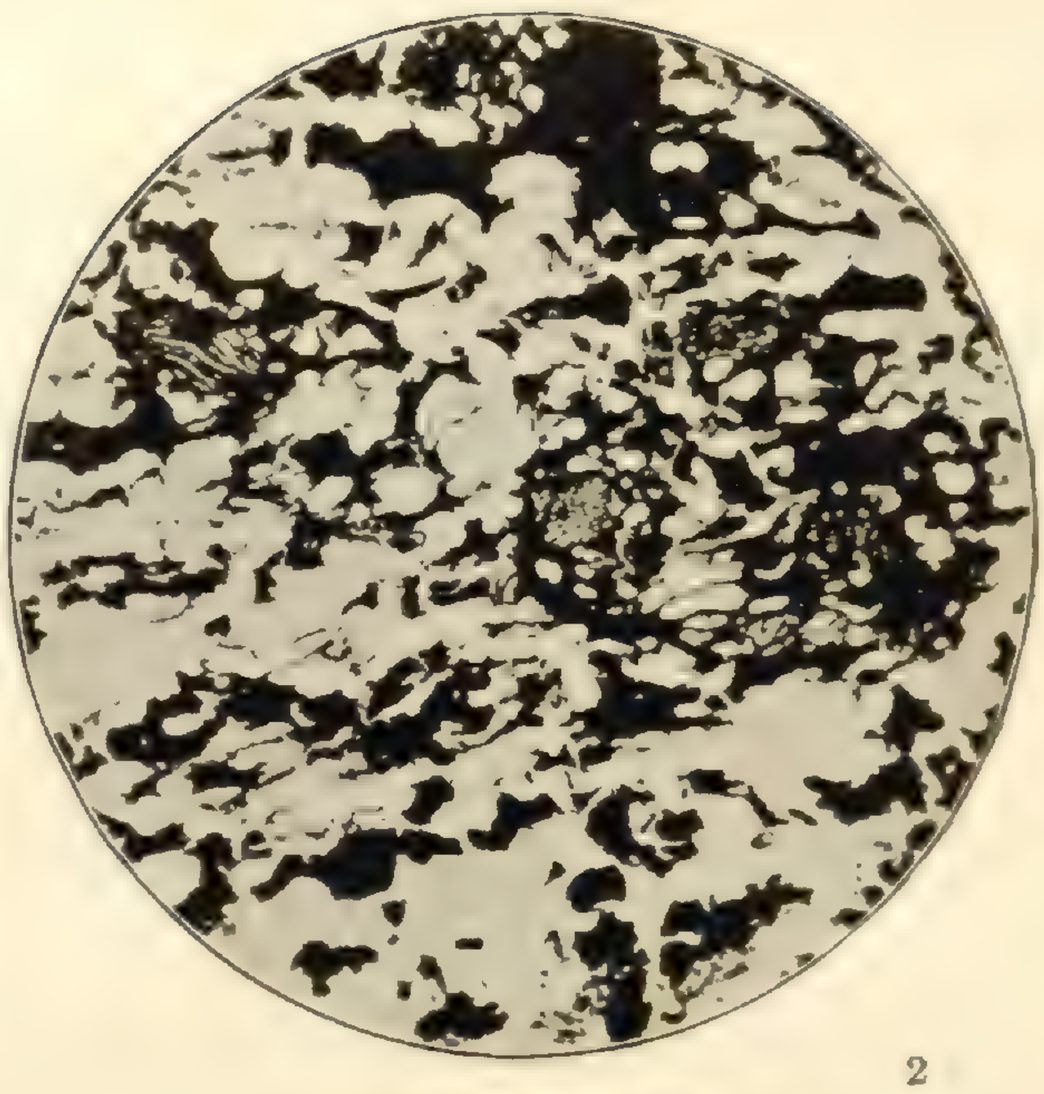

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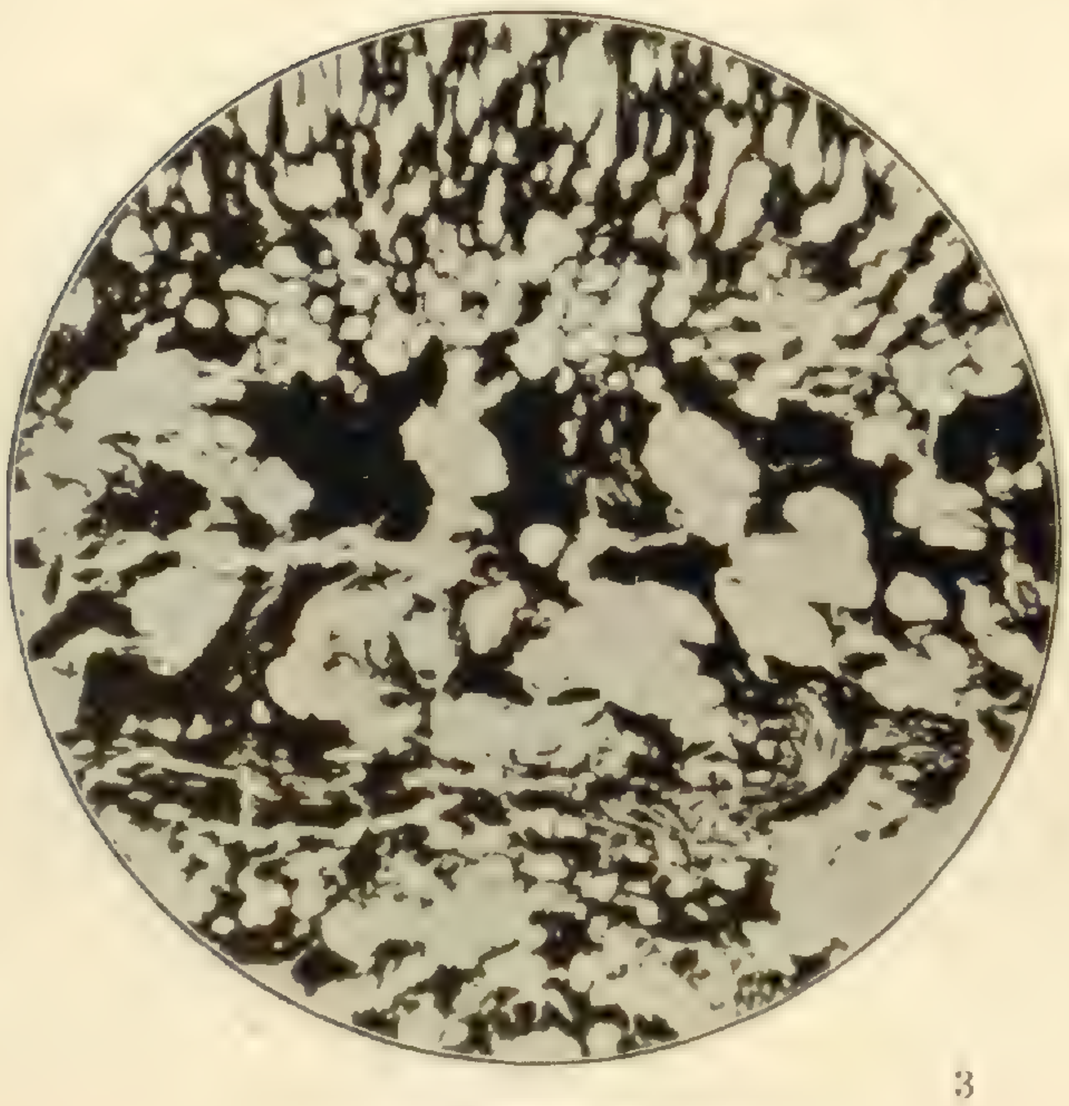

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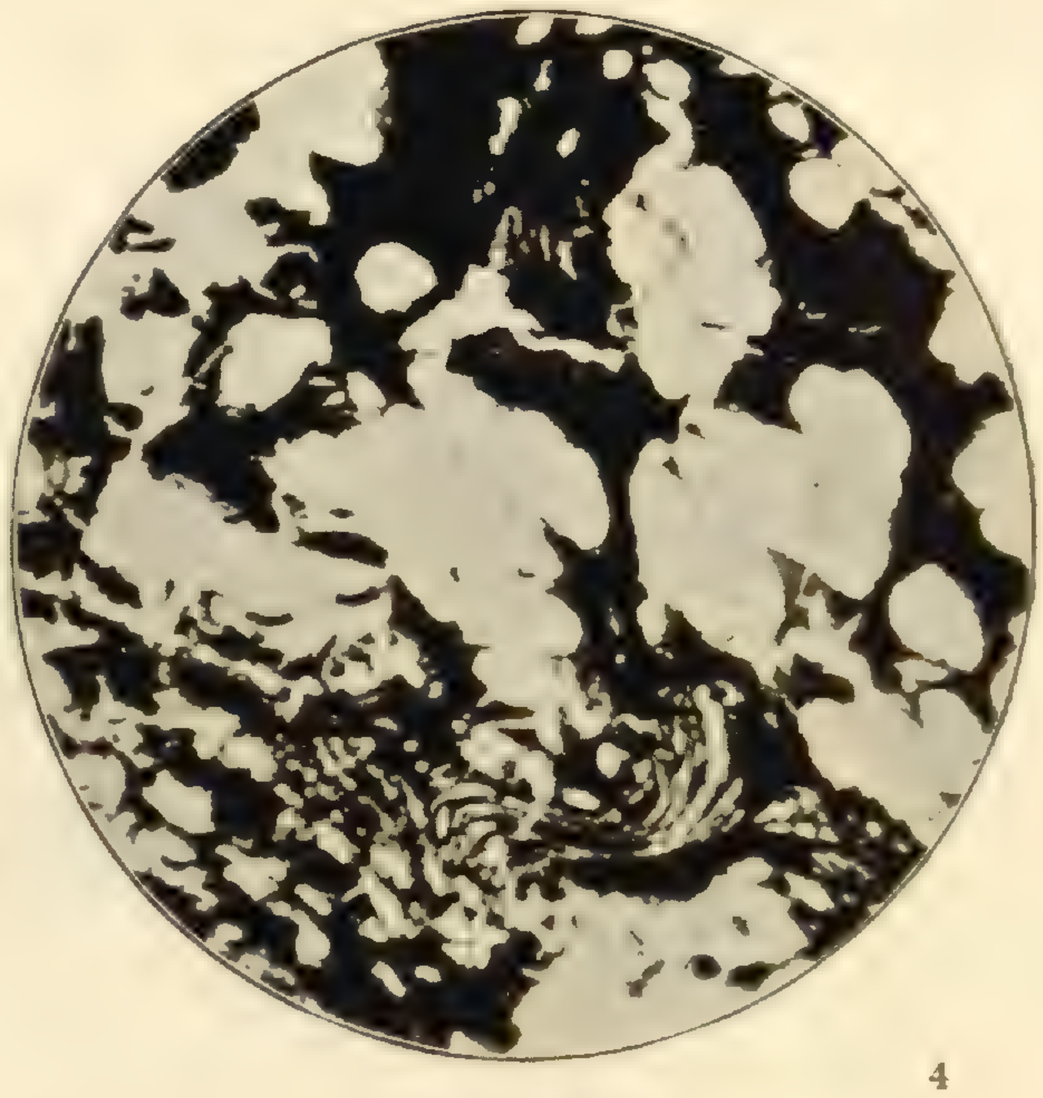

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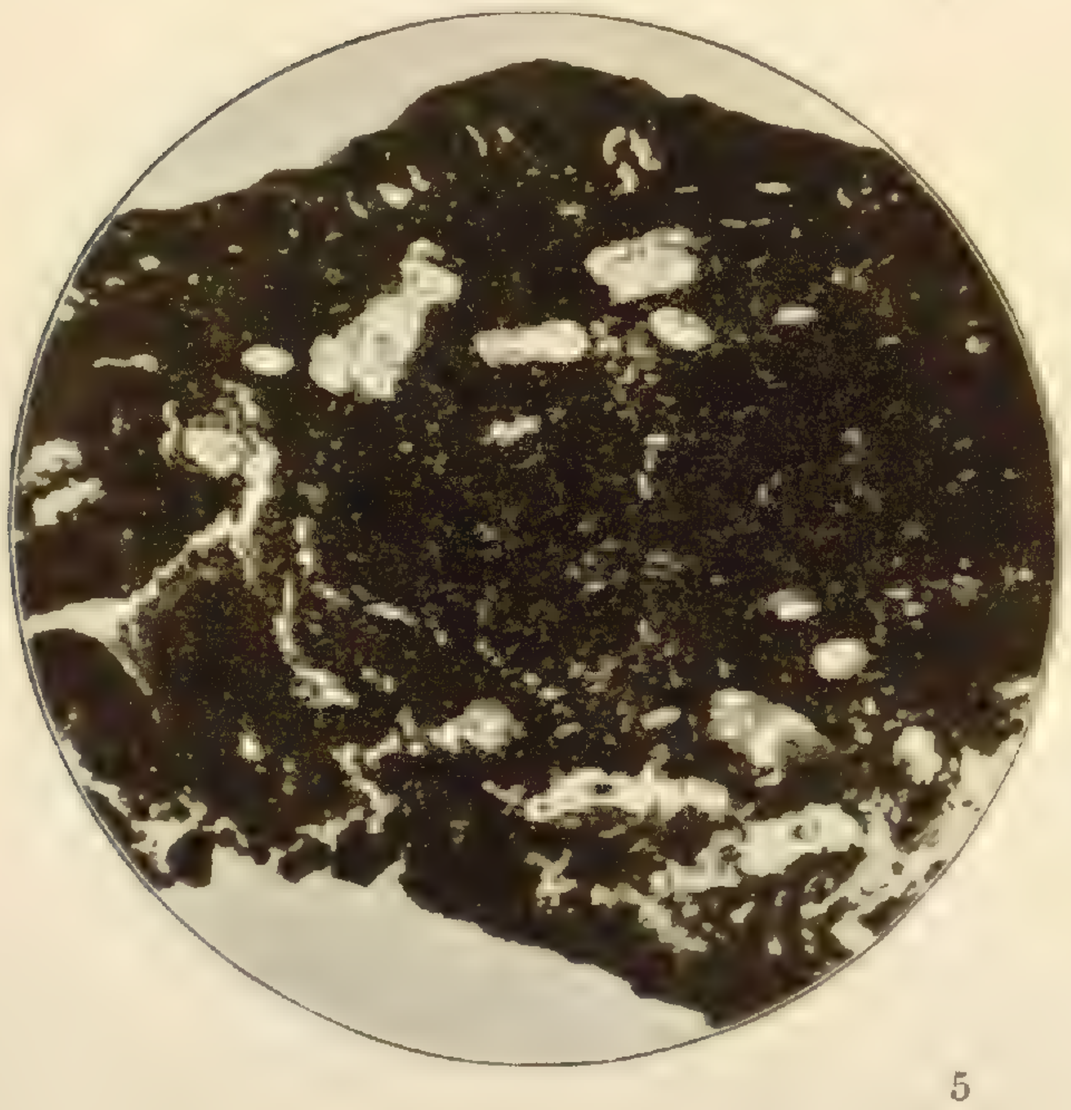

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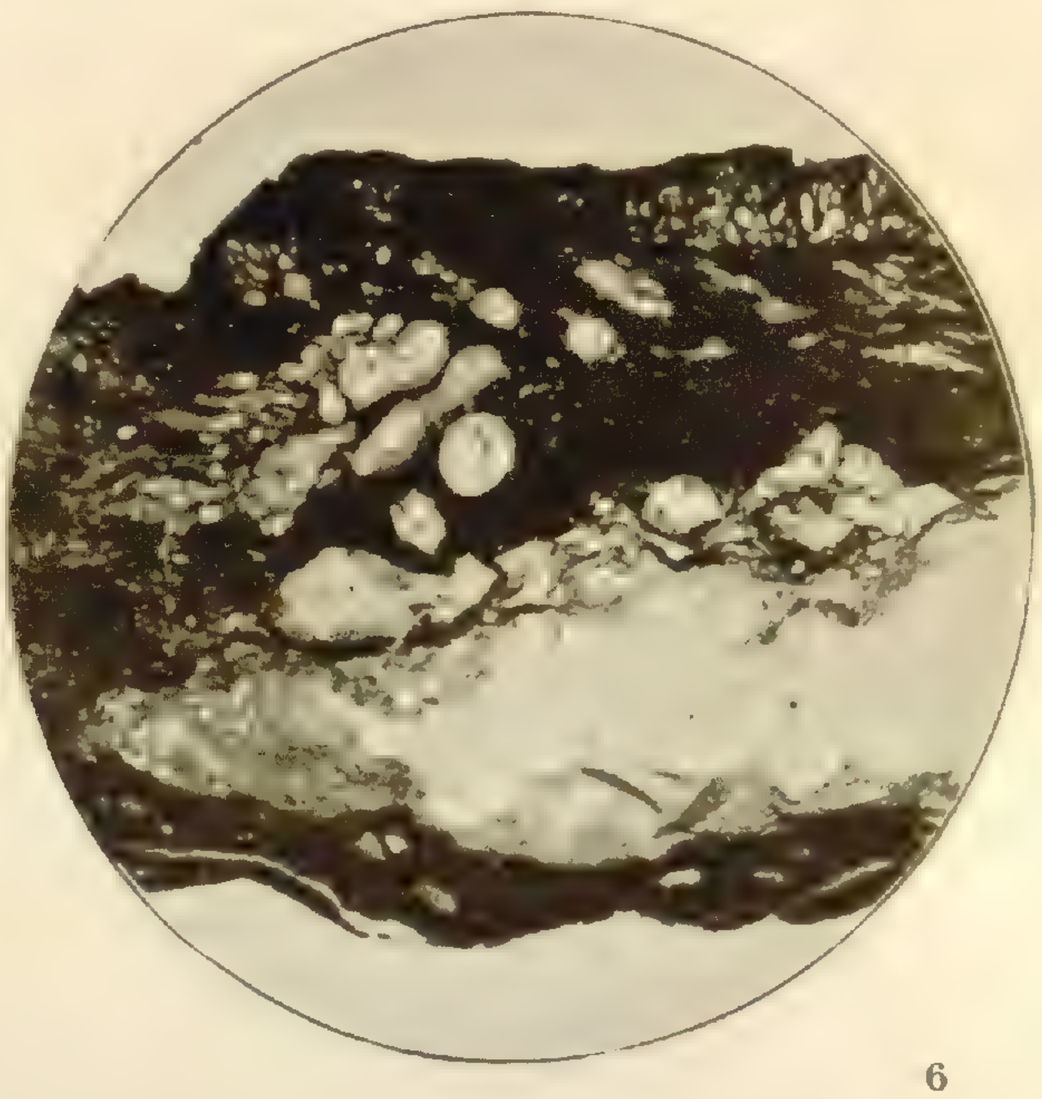

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PLATE 5

FIGS. 1–4.— *Brachyphyllum macrocarpum* Newb., enlarged. Kreischerville, Staten Island, N. Y

Fig. 1.— Longitudinal radial section showing the radial pits of the tracheids, × 200.

Fig. 2.— Medullary ray showing the characteristic Araucarian lateral pits of the ray cells, × 200.

Fig. 3.— Transverse section of the xylem and phloëm in a yearling branch, × 200.

Fig. 4.— Transverse section of a young branch showing the xylem and phloëm, × 200.

FIGS. 5, 6.— *Araucarioxylon* sp., enlarged. Kreischerville, Staten Island, N. Y.

Fig. 5.— Transverse section of injured wood, × 50.

Fig. 6.— One of the traumatic resin canals of the same, × 150.

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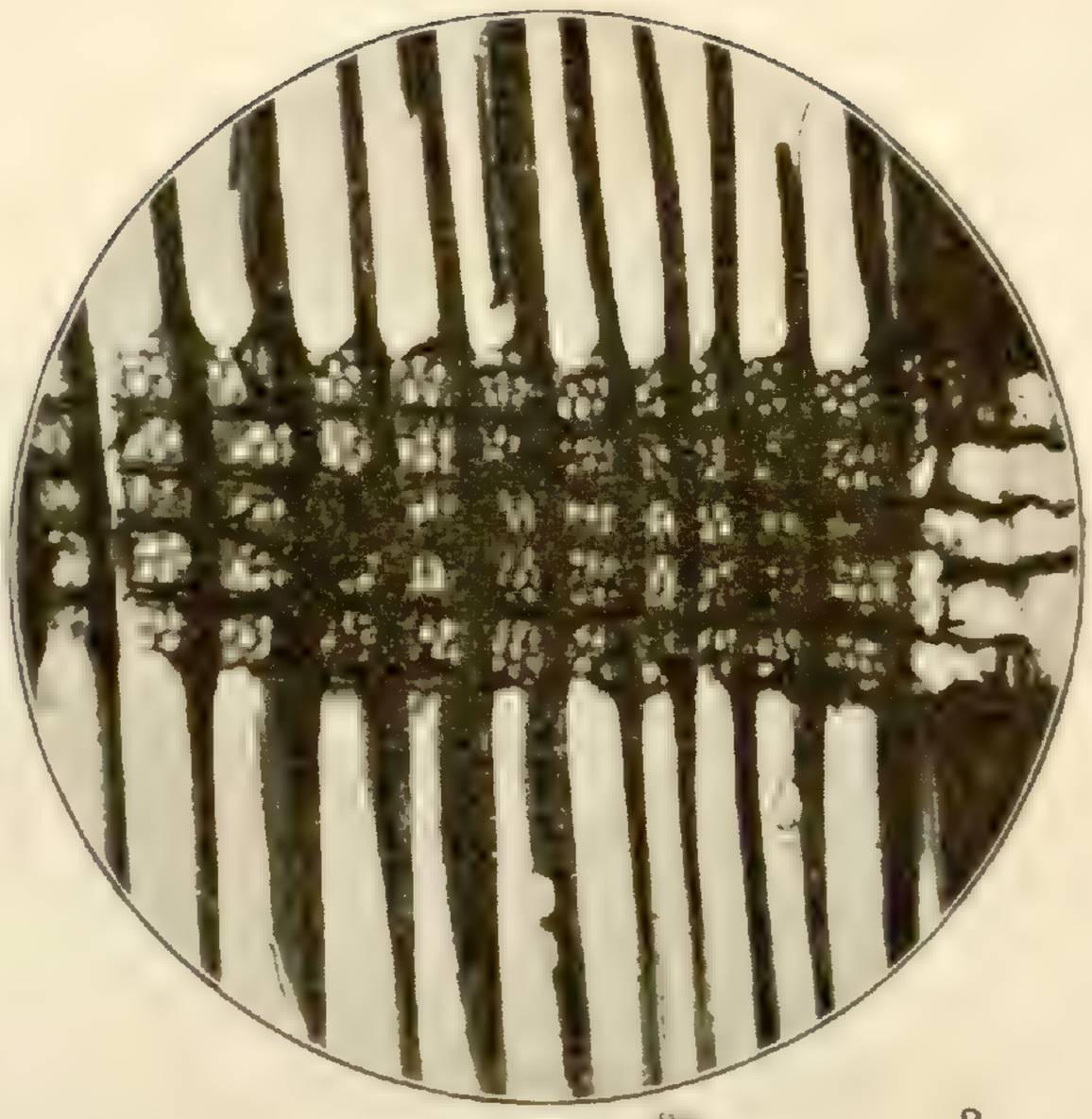

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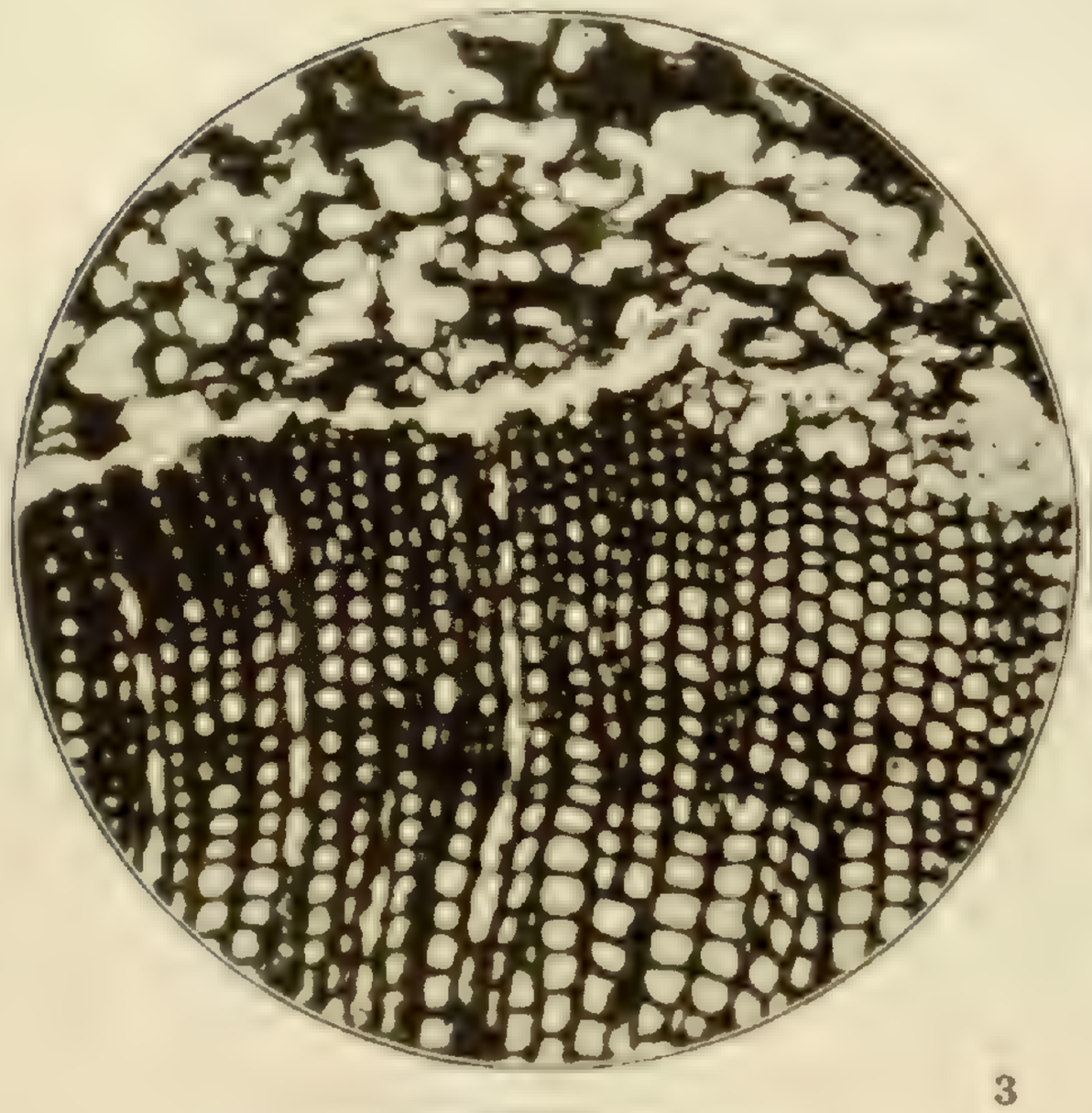

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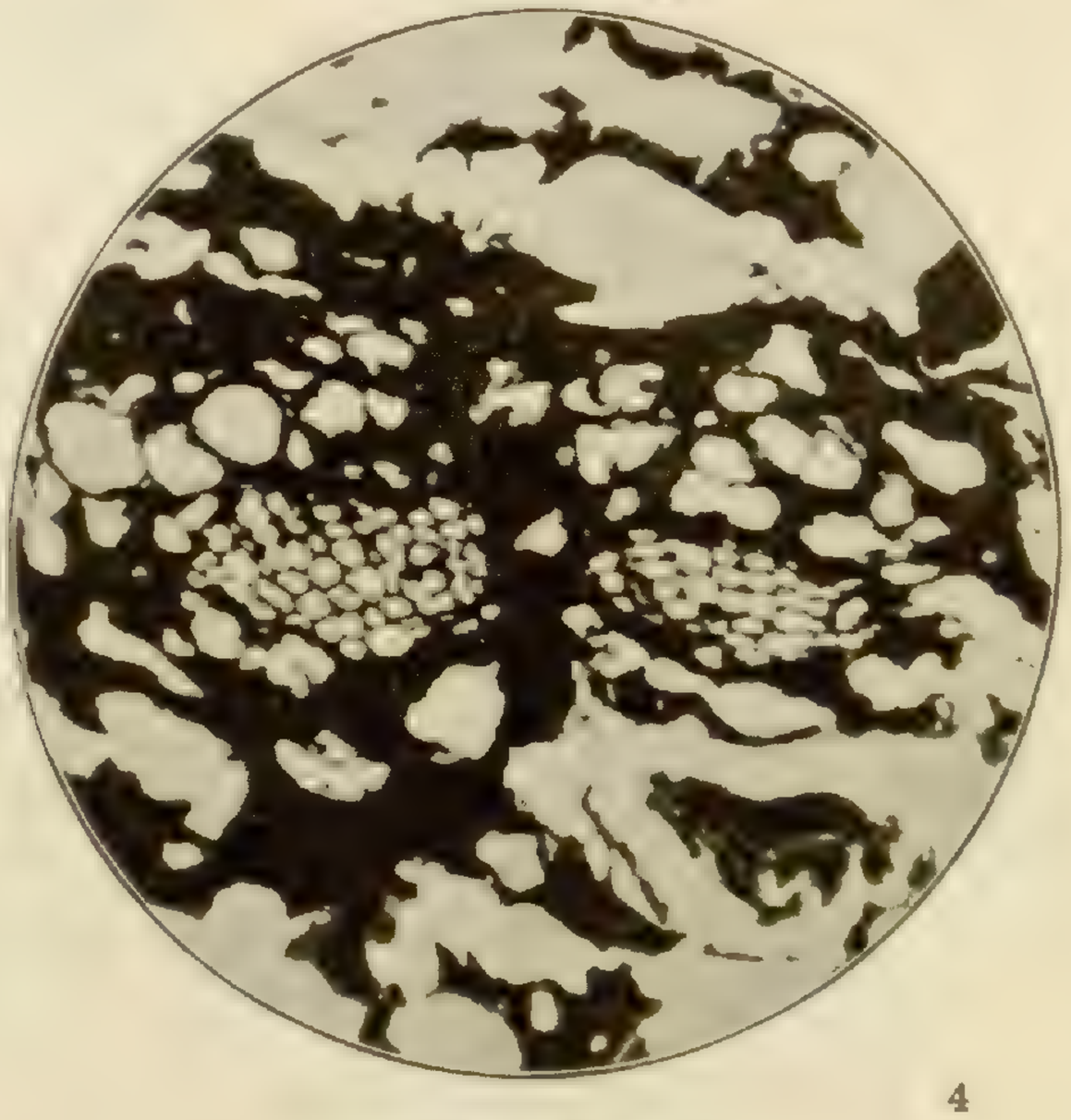

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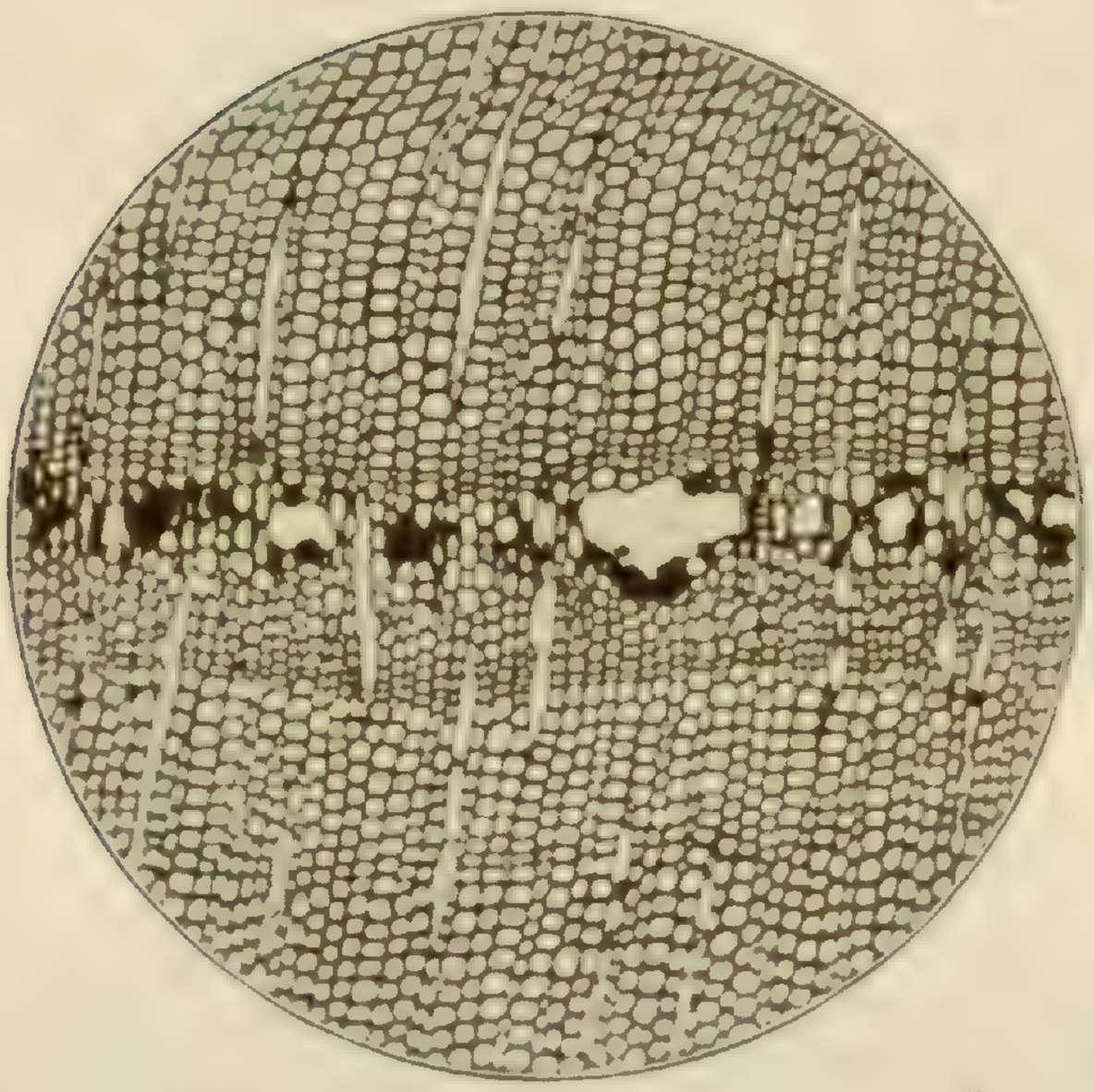

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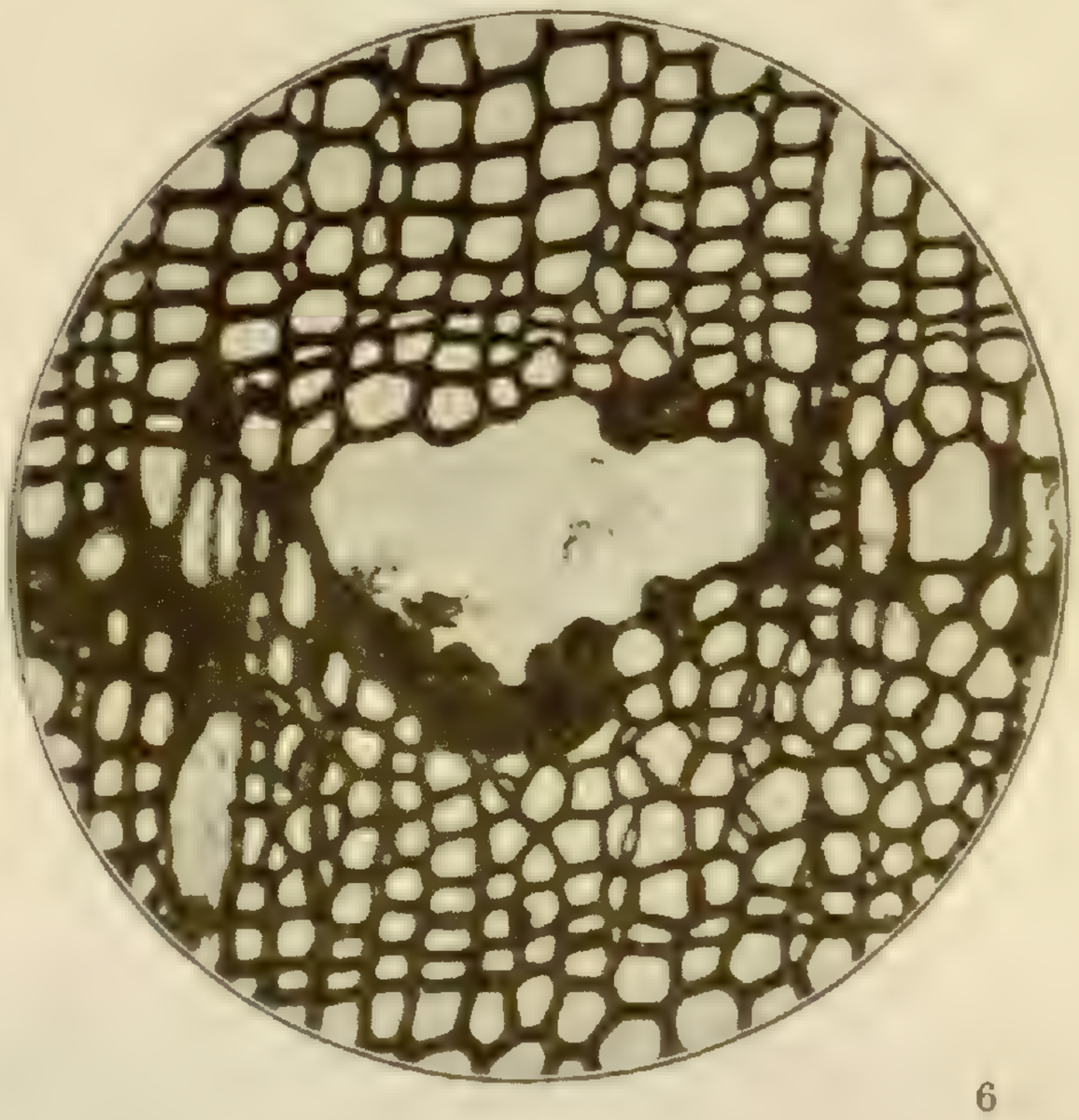

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A NEW PYCNOGONID FROM THE BAHAMAS

LEON J. COLE

Mr. Thomas Barbour has kindly turned over to me for examination a single pycnogonid taken upon the expedition made by himself, in company with Dr. G. M. Allen and Mr. Owen Bryant, to the Bahama Islands in the summer of 1904. A general narrative of their cruise has been published privately by Allen and Barbour (:04). The present paper constitutes the seventh of a series based upon the specimens collected by them.

It would appear from the fact that only a single pycnogonid was taken during this trip, and that none has been reported from the collections of previous scientific expeditions to the same region, that this group must be poorly represented in the waters contiguous to the Bahamas. And in this connection it is interesting to note that the specimen under consideration belongs without doubt, in its systematic relationships, with two species which Dohrn ('81) described from the Gulf of Naples, constituting his genus Barana. This genus is undoubtedly very close to Parazetes, established by Slater ('79) for a pycnogonid from Japan, and possibly should be united with it. The chief difference appears to be the possession by Parazetes of only 9 joints in the palpi, but this is of the less importance when one considers that it is apparently the terminal joint which is lacking, and that the other joints have about the same relative proportions that they have in Barana. Slater lays emphasis on the point that in his specimen the proboscis was 4-cleft; but since the trimerous proboscis is almost universal [1] in all other known Pycnogonida, it is not unreasonable to suppose that he might have had a specimen possessing an individual abnormality. Unfortunately he gives no figures, which would greatly have facilitated the comparison of Parazetes with other

[1] In *Rhynchothorax mediterraneus* O. Costa the proboscis is said to consist of but two antimeres, owing to the failure of the dorsal antimere to develop (*cf.* Dohrn, '81, p. 211).

pycnogonids. Should later discoveries show these forms to belong properly in the same genus, the name Parazetes will take precedence over Barana.

As Sars ('91, p. 133) remarks, the genus Ascorhynchus is certainly very close to Barana, but Eurycyde appears to be well characterized. It seems to me doubtful that Nymphopsis [1] Haswell ('85) and Alcinous O. Costa ('61) belong in this family (Eurycydidæ).

Barana latipes sp. nov.

Pl. 1, Figs. 1–4; Pl. 2, Figs. 5–11

Type: Adult ♀, Museum of Comparative Zoölogy, no. 6947, Crustacea. Collected by Owen Bryant, from rocky shore, Sweeting's Village, Great Abaco, Bahamas, 22 July, 1904.

Trunk broad, compact, tapering somewhat posteriorly; segmentation well marked, the first three segments conspicuously enlarged dorsally and ventrally at their posterior ends, this enlargement forming almost a knob on the dorsal side. Lateral processes stout, about as broad as long, closely approximated but without touching, and each with a conical protuberance dorsally near its distal end. First trunk segment extending anteriorly from the eye tubercle in an elongate, cylindrical neck, which has distinct processes for the articulation of the palpi and the ovigera, the former at the anterior end, the latter immediately anterior to the processes of the first legs. The neck is prolonged at its anterior end into two sharp conical processes, beneath which the chelifori arise. Trunk and all its processes almost smooth and unarmed.

Caudal segment (Pl. 2, Fig. 7) elongate, horizontal, enlarged distally, and sparsely armed with a few scattered small spines; about as long as neck anterior to the processes for the ovigera.

Eye tubercle situated at the base of the neck and midway in the length of the first trunk segment; rather high and pointed forward; consisting of a smaller pointed dome placed on the anterior face of a larger conical elevation (see Pl. 1, Fig. 2). Eyes dark; in the smaller dome.

[1] More fully characterized by Schimkewitsch ('87, p. 128).

Proboscis large, trimerous, with three distinct lips at the tip (Pl. 2, Fig. 6); it arises from the ventral side of the neck at its anterior end, and is directed downwards and backwards, in which position it reaches back to the posterior border of the second trunk segment (see Pl. 1, Fig. 2). In outline it is seen to be fusiform, but is divided at about its distal third by a distinct groove; the basal part does not, however, constitute a distinct segment as in Eurycyde. The proximal portion expands rather regularly to its outer end, while the distal portion taken by itself is distinctly pear-shaped. In cross section, or as viewed from the end (Pl. 2, Fig. 6), the proboscis is triangular, the dorsal angle being directed downward as the organ is carried turned back under the body.

Chelifori (Pl. 1, Fig. 3) short, 2-jointed,[1] and armed with a few small, scattered spines. The basal joint, which expands somewhat distally, is only about as long as the breadth of one of the lateral processes, while the second joint is merely a minute rounded knob. No indication could be seen of a former chelate condition, though these organs undoubtedly possess chelæ in the larva.

Palpi (Pl. 2, Fig. 11) arising from small lateral processes at the anterior end of the neck; 10-jointed; joints 1 and 2 very short; joints 3 and 5 about equal in length, and much the longest of all; the former expands rather gradually distally, while the latter is broadest near its proximal end. Joint 4 equals in length about one third of joint 5; joint 6 is still shorter and bends at a right angle to 5; joint 7 is slightly longer than joint 6, and the succeeding joints, 8, 9, and 10, decrease gradually in size. These distal four joints normally lie in nearly a straight line and parallel with joint 5, and reach back about two thirds of its length. The first five joints are sparsely armed with small spines, which become more numerous, however, at the distal end of joint 5,

[1]Carpenter (: 05, p. 4) maintains with good reason that each of the parts of the chela, when present, should be counted as a joint. Without explanation, however, such a nomenclature is apt to introduce confusion, especially in those cases where the movable finger is reduced to the merest knob or projection on the palm, or may apparently disappear completely, as in the case of the species here described.

and are thickly set on the outer sides of all the succeeding joints, where they are about equal in length to the diameter of the joints. The whole palp, if extended straight backward, would reach about to the base of the caudal segment.

Ovigera (Pl. 2, Fig. 9) 11-jointed;[1] about a third longer (in the female) than the palp, the length to the principal flexure, between the fifth and sixth joints, being, however, almost exactly equal to the length of the palp to the corresponding place. Joint 1 short; joints 2 and 3 about equal in length, and longer than joint 1; joints 4 and 5 each slightly more than twice as long as joint 2 or 3; joint 6 bent backward upon joint 5, and only a little more than half as long; joints 7, 8, 9, and 10 grow successively smaller, both in length and in diameter; this part (the "terminal part") of the oviger is usually somewhat flexed. The terminal claw, which constitutes the eleventh joint of the appendage, is small and curved. The first four joints are practically free from hairs or spines; a few scattered short spines occur on joints 5 and 6; joints 7 to 10 are armed with three or four series of denticulate spines with deeply incised margins. These spines are longer on one side of the joint, and become smaller in each of the longitudinal rows as one moves across to the other side (Pl. 2, Figs. 9 and 10). Each of these joints has in addition near its distal end a rather strong simple spine. At the middle of the fourth joint is a prominent knob-like protuberance, which probably carries the opening of what Dohrn ('81, p. 123) calls the excretory organ.

Legs rather stout, somewhat less than twice as long as body from anterior end of neck to tip of caudal segment. Coxal joints (Pl. 2, Fig. 8) all short and broad, the second being a little longer than the first and third, which are about equal. The femur and first tibial joint are each a little shorter than the three coxal joints together, while the second tibial joint is slightly longer than the coxal region. Femur broadest, being about a third as long as broad; tibial joints narrower. These joints are flattened from side to side, so that the ventral margin forms rather a sharp edge.

[1] I agree with Dohrn ('81, p. 123) that the terminal claw should be counted as a joint.

First tarsal joint short, squarish, bilobed distally; second tarsal joint four to five times as long as broad, its inner (ventral) border only slightly curved, the outer (dorsal) somewhat more arched (Pl. 1, Fig. 4). Claw short and rather stout, less than a third the length of the second tarsal joint; somewhat curved towards the tip; auxiliary claws wanting. The coxal and femoral joints are only sparsely armed with short spines, which become longer and more numerous on the tibial and tarsal joints, especially long bristles (about as long as the breadth of the segments) occurring along the dorsal margins of the second tibial and second tarsal joints. On the ventral side of the second tibial joint near its distal end begin a number of thickly set short spines, which become more numerous on the tarsal joints and give to them a comb-like appearance. No "heel" is developed on the foot.

A few ova could be distinguished in the femoral joints, and the openings of the oviducts could be seen in the usual position on the ventral side of the second coxal joints of the second, third, and fourth legs, and they were probably present also on the first pair although they could not be made out.

Color in alcohol yellowish or light brown.

Measurements

Extent	14 or 15 mm.
Length, anterior end of neck to tip of caudal segment	3.8 mm.
Length of proboscis	2.2 mm.
Length of caudal segment	1.0 mm.
Length of cheliforus	0.33 mm.
Length of palp	2.8 mm.
Length of oviger	3.5 mm.

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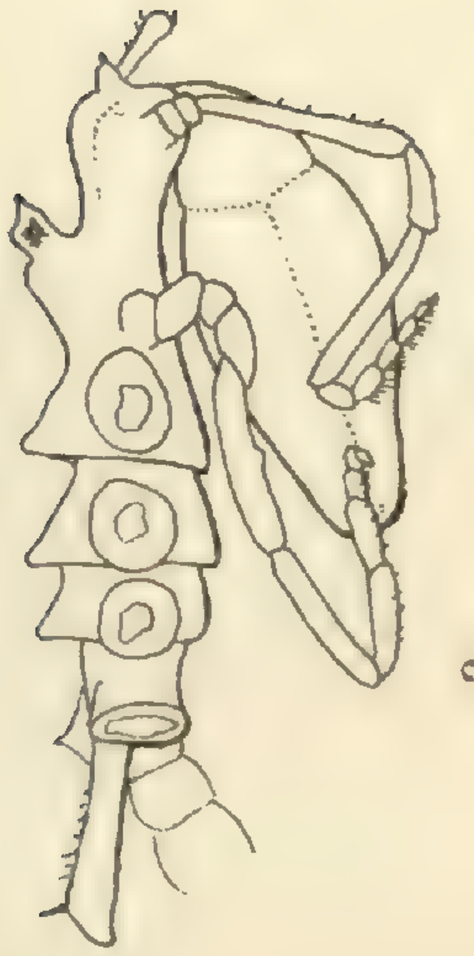
PLATE 1

Barana latipes sp. nov., female

(All figures drawn with Abbé camera)

FIG. 1.— Dorsal view. × 12.
FIG. 2.— View from right side, the legs of that side removed. × 12.
FIG. 3.— Left cheliforus. × 50.
FIG. 4.— Foot of second leg of right side. × 50.



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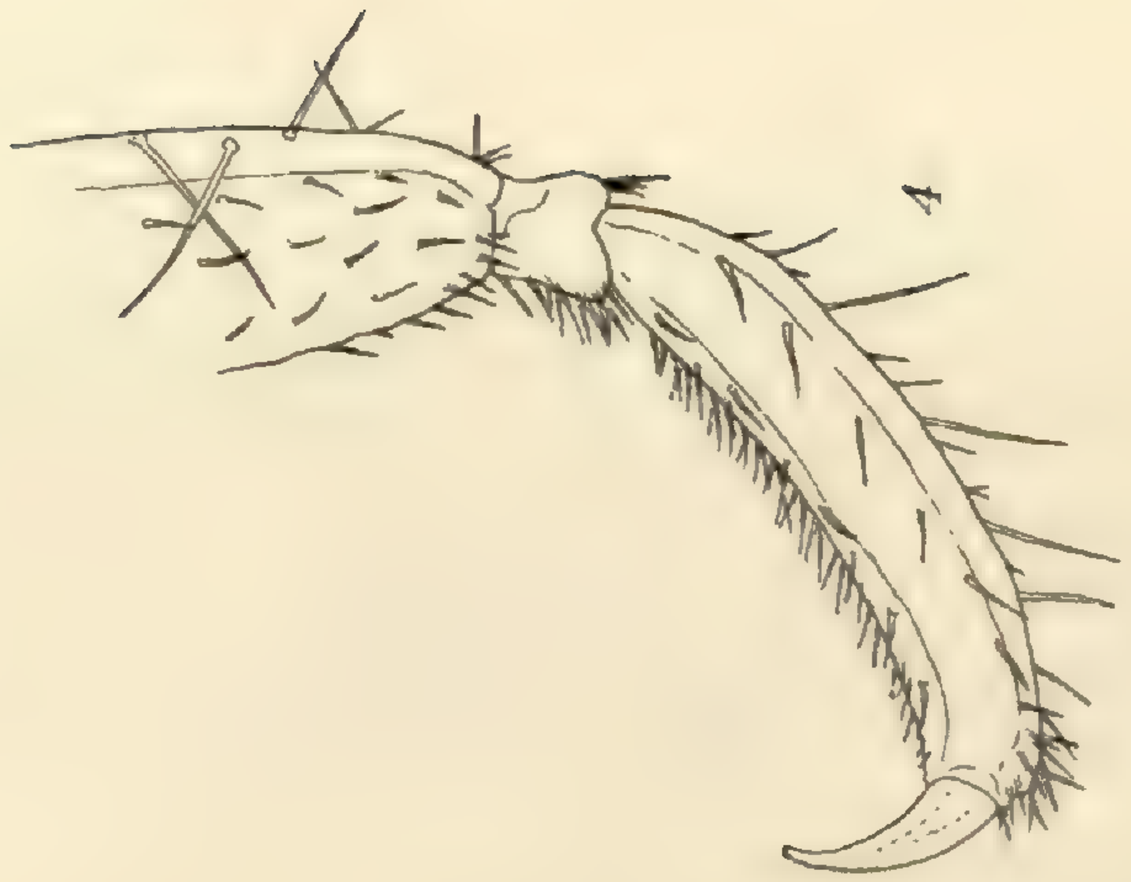

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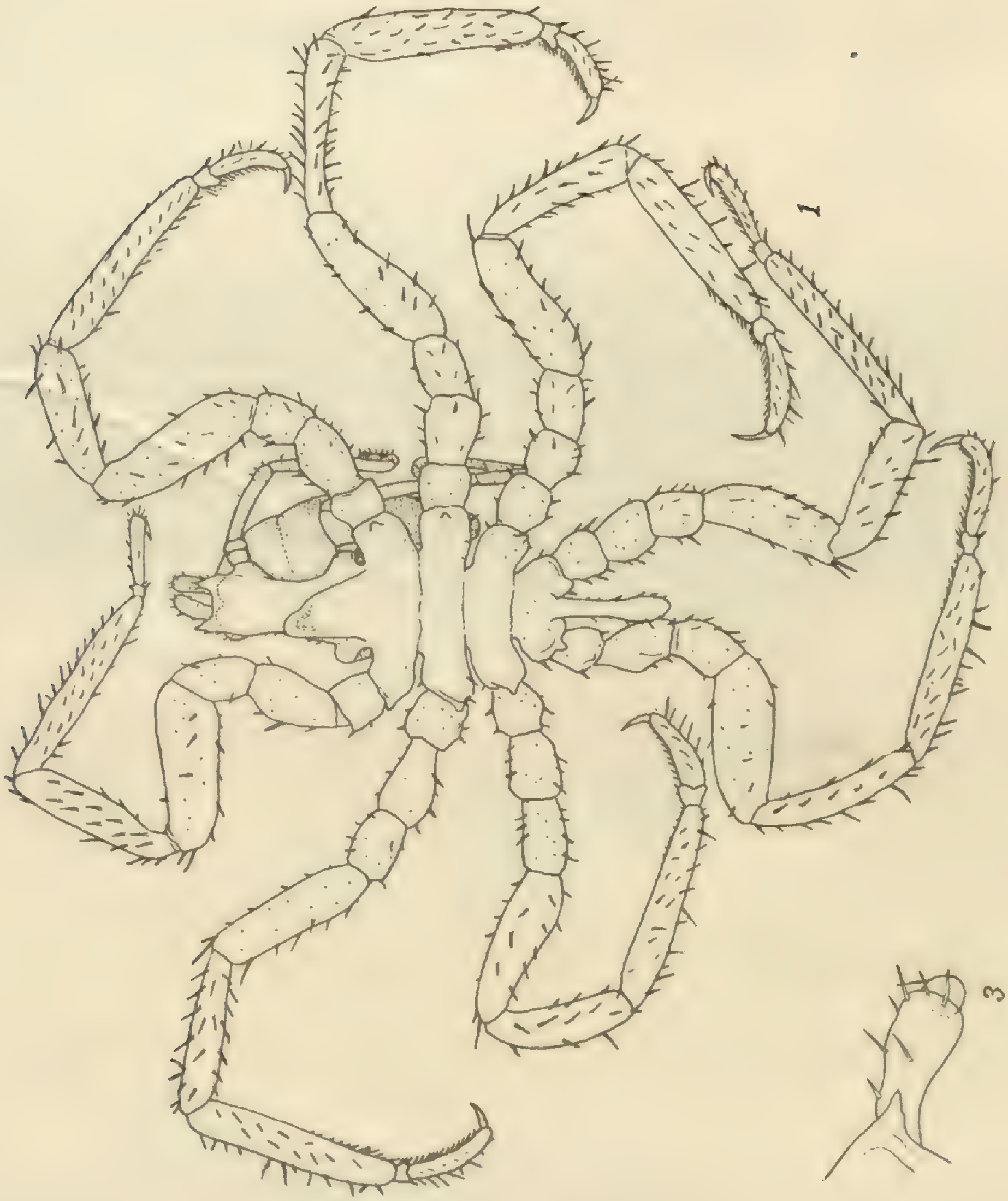

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PLATE 2

Banara latipes sp. nov., female

(All figures except Fig. 6 drawn with Abbe camera)

FIG. 5.— Trunk and proboscis, with right cheliforus, palp, and oviger, as seen from below. These appendages have been removed from the left side. × 16.

FIG. 6.— Proboscis viewed directly from the end.

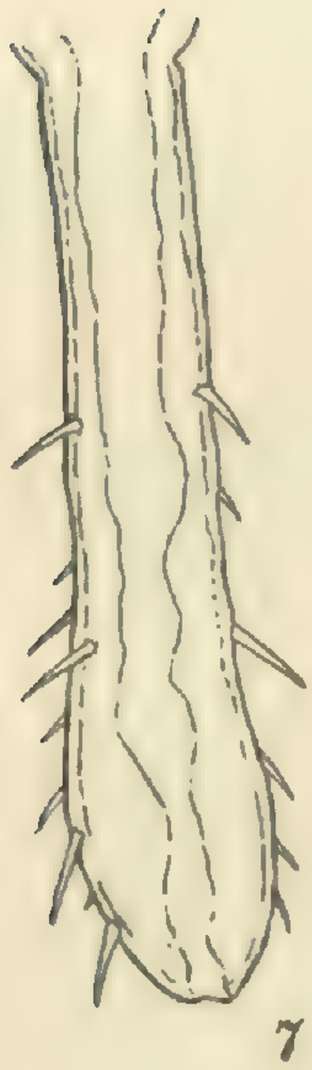
FIG. 7.— Caudal segment from above (dorsal view). × 50.

FIG. 8 — Coxal joints of second right leg; *o*, position of external genital opening. × 20.

FIG. 9.— Oviger of left side; *v*, row of spines shown enlarged in Fig. 10. × 50.

FIG. 10.— Row of denticulate spines marked *x* in Fig. 9. × 213.

FIG. 11.— Palp of left side. × 50.



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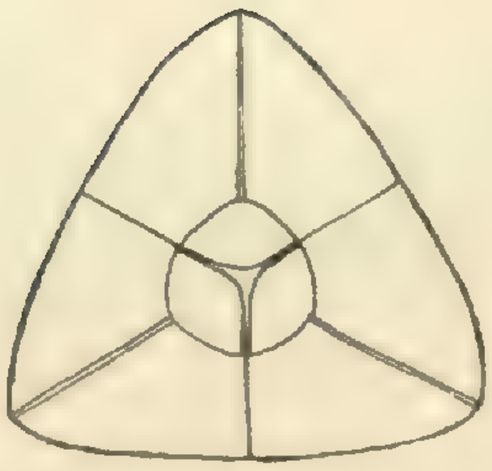

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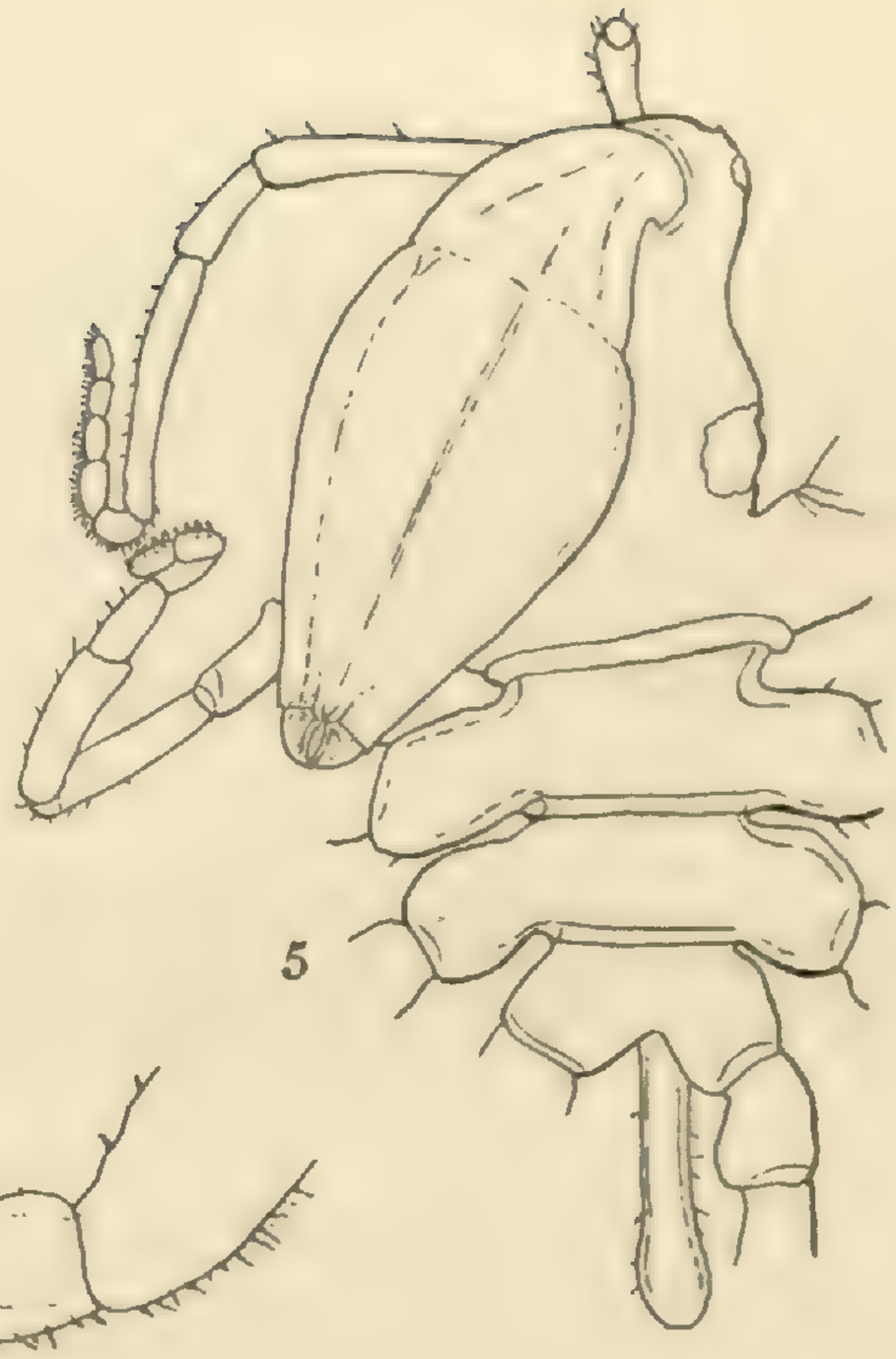

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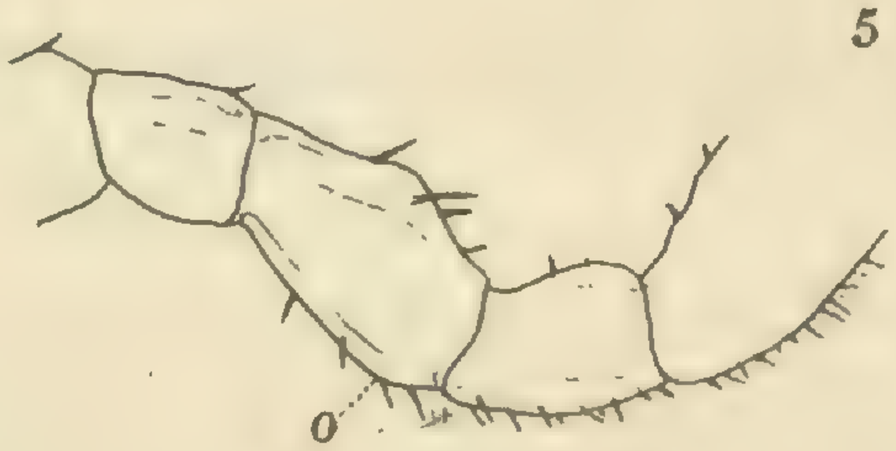

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ADDITIONAL NOTES ON BAHAMA SNAKES

THOMAS BARBOUR

THE specimens which form the basis of this paper are now all the property of the Museum of Comparative Zoölogy at Cambridge, Mass.

In December, 1904, a paper[1] was published in which a good series of lizards but rather few snakes were reported on. Now an opportunity is presented to offer notes on about forty specimens of Ophidians, for last winter Mr. A. E. Wight collected a number of fishes and reptiles during February and March; while later Gustav Sabille returned to New York from Nassau with an interesting lot of living snakes. These were also purchased and advantage has been taken of this opportunity to study the species while yet alive. Five examples of the New Providence Island Boa from five to perhaps eight feet long have been presented to the New York Zoölogical Society. They are still alive in the Reptile House at Bronx Park, where shortly after their arrival two specimens simultaneously gave birth to thirty-eight young. I regret that I do not know the number in each litter. Mr. R. L. Ditmars has also told me that several specimens of *Alsophis vudii* ate a few Ungualiæ which were in the same case and have refused other food.

Since the afore-mentioned paper was published, Dr. Leonhard Stejneger has published an excellent analysis of the herpetology in a volume[2] on the Bahamas edited by Dr. Shattuck of Baltimore. In general I agree very heartily with Dr. Stejneger's conclusions, but doubt whether *Typhlops lumbricalis* will ever be found on New Providence. I, as well as others, have searched carefully for it on this island and have never heard of its occurrence. With

[1]Barbour, Thomas. "Batrachia and Reptilia from the Bahamas." *Bull. Mus. Comp. Zoöl.*, vol. 46, no. 3, pp. 55–61.

[2]*The Bahama Islands.* Edited by George Burbank Shattuck. The Geographical Society of Baltimore; New York, The Macmillan Co., 1905, xxxii + 630 pp., plates and text figs.

far less opportunity to hunt for it carefully I obtained a specimen near Marsh Harbor, Abaco, on July 6, 1904. I imagine that for some unknown reason this species has skipped New Providence in its northward progression, as *Liocephalus carinatus* appears to have done, though, to be sure, the species has not yet been taken on any island except on Great Abaco.

For the Northern Bahaman Boa Boulenger's and Stejneger's application of Fischer's name is undoubtedly correct.

Epicrates striatus Fischer.

E. strigilatus Cope. Barbour, *Bull. Mus. Comp. Zoöl.*, vol. 46, p. 59.

Six specimens just born, and one considerably older; all New Providence Island stock. The very young ones are about $14\frac{1}{4}$ inches long; the tail takes up $2\frac{3}{4}$ inches of this length. The color of these young is considerably lighter than that of adults, the opalescence is if anything more marked. One specimen is diffusely blotched with white laterally.

An older specimen measures $28\frac{1}{2}$ inches in total length but part of the tail is gone. This example is much darker in color than the small ones. The pattern is the broken irregular one which is characteristic of the adults of the species. In the very young ones, on the other hand, there is a dorsal series of light blotches separated by darker; below this laterally there is a light chestnut stripe very iridescent; below this again are three darker stripes, the uppermost lightest, the middle one darkest. Between these are two light bands, the upper one buffish, the lower one almost white. The bellies are ivory white.

The natives call this the "fowl snake." The squamation of this species is typically so variable that the counts of these specimens are of no especial interest.

Ungualia pardalis Gundlach.

Six specimens, all from New Providence Island. One of these is younger than any examined heretofore.

In my previous paper the dichromatism of this species was mentioned. This is also shown very well among these specimens. One about $12\frac{1}{2}$ inches long is almost uniform buffish brown above with a lateral row of small darker markings. A few dark markings are on the gastrosteges, which are yellow. The tail is blackish above for one inch, below for less than $\frac{1}{4}$ inch. Two other specimens of about the same size are slaty blue with two dorsal rows of squarish darker blotches. Between these pairs of markings is a narrow very light band. Two others are brown with a double row of dorsal markings. The sixth, and smallest, is $5\frac{1}{4}$ inches long. It is slate-colored, the dorsal markings are fused. There is a very distinct lateral row of squarish spots and on the gastrosteges posteriorly there are two rows of dark spots generally in pairs. The distal $\frac{1}{2}$ inch of the tail is bright yellow with the extreme tip black. Previously it has been noted that the amount of black on the tail seemed correlated with age. The scale counts of these specimens are given in the same order as that in which they have been mentioned:—

Sc. $\frac{13}{152+31}$; $\frac{25}{149+31}$; $\frac{23}{152+30}$; $\frac{23}{157+33}$; $\frac{23}{153+31}$; $\frac{23}{153+33}$

The natives call these "thunder snakes," because they say that they frequently crawl about after severe rain storms.

This species is most frequently taken among the heaps of broken rock which are piled about the trunks of orange trees; or under stone walls. I have never seen one above ground.

Alsophis vudii Cope.

Twenty-four specimens, all from New Providence Island.

The largest specimen is 43 inches in total length with the tail 12 inches long. The smallest is about 21 inches long, with the tail nearly one third of the total length.

The color of this species is vastly more variable than published descriptions and material previously examined, had suggested. One large one about 40 inches long, has the head and neck mottled black and rich reddish brown. There is a black stripe on each side of the neck. The color gradually changes until the posterior

half of the creature is deep lustrous brown-black. Another specimen is brick red above and almost salmon-color below. Still another is uniform ashy gray above, marbled with darker below. The top of the head is richly puncticulate with black and red-brown. There is a dark stripe through the eye, also several dark blotches on the neck region above. A number of specimens are rich chocolate brown both above and below, often with a light-edged dark stripe running through the eye. Several examples are brown above and pinkish beneath. The last specimen which I shall mention is dark iron-gray anteriorly, shading posteriorly into olive-brown. This one also has a light-edged dark stripe through the eye.

The Cuban specimens of *A. angulifer* do not show such variation. I can but think that the Bahaman examples are worthy of specific distinctness.

The natives call this "chicken" or "whip snake." I have added the scale counts of these individuals thinking that perhaps they may be of use for comparison when someone procures a large series of the Cuban form. It is remarkable how many of the tails are imperfect.

New Providence Island specimens:—

$$\frac{17}{170+108};\ \frac{17}{165+\ ?};\ \frac{17}{109+\ ?};\ \frac{17}{165+104};\ \frac{17}{167+105};\ \frac{17}{164+\ ?}$$

$$\frac{17}{169+?};\ \frac{17}{166+107};\ \frac{17}{159+112};\ \frac{17}{169+111};\ \frac{17}{162+\ ?};\ \frac{17}{171+19}$$

$$\frac{17}{163+116};\ \frac{17}{163+101};\ \frac{17}{165+109};\ \frac{17}{168+110};\ \frac{17}{170+107};\ \frac{17}{165+117}$$

$$\frac{17}{165+106};\ \frac{17}{166+?};\ \frac{17}{164+119};\ \frac{17}{170+111};\ \frac{17}{169+113};\ \frac{17}{162+119}$$

Other specimens in the Museum collection show the following scale counts:— $\frac{17}{167+?};\ \frac{17}{170+101};\ \frac{17}{164+118};\ \frac{17}{161+\ ?}$

The four following are from Andros. Island:—

$$\frac{17}{171+121};\ \frac{17}{166+?};\ \frac{17}{161+?};\ \frac{17}{164+118}.$$

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CONTENTS

			Page
I.	Fresh-water Copepoda of Massachusetts	A. S. PEARSE	241
II.	Variations in the Pollen Grain of *Picea excelsa*	DR. J. B. POLLOCK	253
III.	Anatomy of *Cryptobranchus allegheniensis*	PROFESSOR A. M. REESE	287

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THE

AMERICAN NATURALIST

VOL. XL *April, 1906* No. 472

FRESH-WATER COPEPODA OF MASSACHUSETTS

A. S. PEARSE

IN her excellent review of the Crustacea of New England, Miss Rathbun (:05) lists nine species of fresh-water copepods for Massachusetts, as follows: —

? *Heterocope* sp.
Cyclops vernalis Fischer.
Cyclops bicuspidatus Claus.
Cyclops serrulatus Fischer.
Cyclops phaleratus Koch.
Diaptomus leptopus Forbes.
Cyclops viridis insectus Forbes.
Cyclops albidus (Jurine).
Cyclops prasinus Fischer.

As her paper cites the original description of each of these species and the authority for its occurrence in Massachusetts, these points need not be taken up here. The occurrence of Heterocope in America is doubtful and it cannot properly be included on the evidence that Cragin ('83) offers.

To the above list I am now able to add the following: —

Eurytemora affinis Poppe.
? *Diaptomus ashlandi* Marsh.
Diaptomus pygmæus n. sp.
Cyclops edax Forbes.
Cyclops viridis brevispinosus Herrick.
Cyclops bicolor Sars.
Cyclops fimbriatus poppei Rehberg.
Canthocamptus illinoisensis Forbes.
Canthocamptus northumbricus americanus Herrick.
Epischura massachusettsensis n. sp.
Diaptomus sanguineus Forbes.
Diaptomus spatulocrenatus n. sp.
Cyclops leuckarti Claus.
Cyclops fuscus (Jurine).
Cyclops varicans Sars.
Canthocamptus staphylinoides Pearse.
Canthocamptus minutus Claus.

I have also observed all the species in Miss Rathbun's list except Heterocope and *Cyclops prasinus*. *Eurytemora affinis* has never been observed before in America outside the Gulf of Mexico (Foster, :04). The previous eastern range of *Diaptomus ashlandi* is Indiana; *Diaptomus massachusettsensis* and *Diaptomus spatulocrenatus* are apparently new to science. The ranges of all the species of Canthocamptus here listed, are considerably extended. The ranges of several species of Cyclops are widened somewhat but this is of no very great significance as it is a cosmopolitan genus and all the species have been previously found in the United States.

My thanks are rendered to J. A. Cushman for specimens from various stations and for collections from Nantucket Island which were made by Mariana Hussey, E. W. Morgan, and S. D. Richmond. I am also indebted to I. L. Shaw for specimens from Brookline, Wellesley, and Randolph.

The types of the new species here described have been presented to the Boston Society of Natural History.

Genus EURYTEMORA Giesbrecht

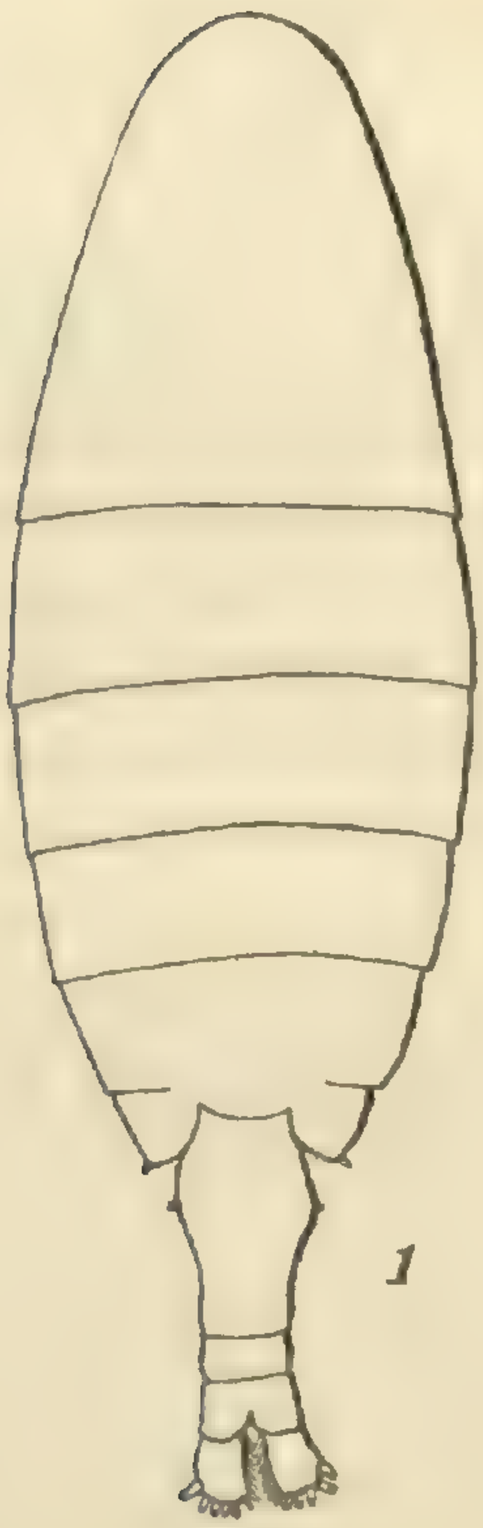
Eurytemora affinis Poppe.—This species occurred in a collection from Squam Pond, Nantucket Island, made by S. D. Richmond, June 4, 1905.

Genus EPISCHURA Forbes

Epischura massachusettsensis n. sp.

This species is described from nine females collected by I. L. Shaw at Wellesley, Mass., April 20, 1905. No males were taken at that time nor in October when several dredgings were made.

Description.— Of medium size, cephalothorax elliptical seen from above, broadest about the middle, truncate at anterior end; six-segmented, first segment almost half the cephalothorax and having a suture at its middle; last segment distinct. Abdomen (Fig. 4) symmetrical, slender, five-segmented (furca included). First segment very short, second segment longest, third segment longer than first but shorter than fourth. Furca twice as long as wide, hairy on inner margin, bearing three strong plumose terminal setæ and a smaller one at both the inner (not plumose) and outer distal angles. Antennæ twenty-five-segmented and when reflexed, extending to middle of furca.



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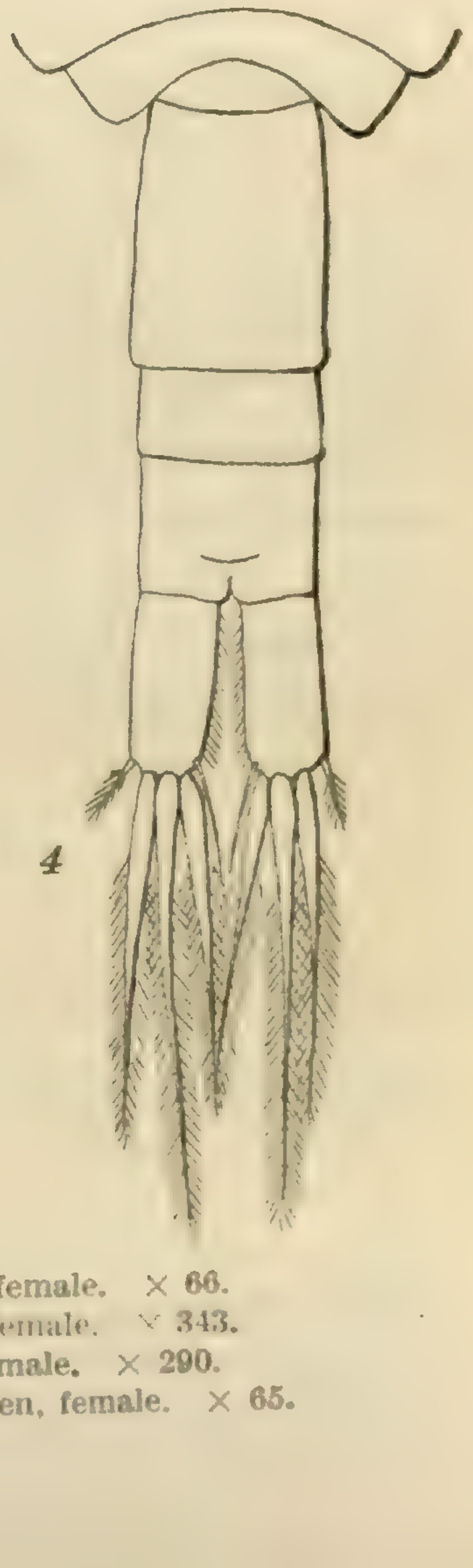

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FIG. 1.— *Diaptomus pygmæus.* Dorsal view of female. × 66.
FIG. 2.— *Diaptomus pygmæus.* Left fifth foot, female. × 343.
FIG. 3.— *Diaptomus pygmæus.* Left fifth foot, male. × 290.
FIG. 4.— *Epischura massachusettsensis.* Abdomen, female. × 65.

FIG. 5.— *Epischura massachusettsensis*. Fifth foot, female. × 155.

Fifth foot (Fig. 5) uniramose, three segmented. First segment about as broad as long, slightly tapering toward its free end; armed at outer distal angle with a slender spine. Second segment two thirds as broad as long, slightly longer than preceding segment, armed on distal end with a sharp spine at outer angle. Third segment half as broad as long and one third longer than second segment, armed on inner margin with three strong acute spines which are denticulate on the outer side; at the apex with three strong spines (middle one denticulate) the innermost of which is longest, being one third the length of the segment; on the outer margin at the distal third armed with a small strong spine.

Length of female 2.04–2.81 mm.

Genus DIAPTOMUS Westwood

? Diaptomus ashlandi Marsh.— A single specimen, doubtfully identified as belonging to this species, was taken at Cambridge, May 5, 1905.

Diaptomus leptopus Forbes.—This species was common from the middle of May to the middle of October. Localities: Cambridge, Medford, Wellesley.

Diaptomus sanguineus Forbes.—Collected at Wellesley and Medford in April and May.

Diaptomus pygmæus n. sp.

Figs. 1–3

Description.— A rather slender species of small size as the name indicates. The cephalothorax (Fig. 1) is widest at the middle; first segment is thrice the length of the following ones, which are about equal; last two segments are confluent above; last segment produced posteriorly and armed on each side with a short acute spine. First abdominal segment dilated laterally and armed on each side with a minute spine; second segment shorter than the third which equals the furca. The furca are two thirds as wide as long and hairy on the inner margin.

Antennæ twenty-five-segmented; in the female reaching beyond tips of furcal setæ and in the male to the ends of furcal rami. Male right antenna not swollen anterior to geniculate joint; antepenultimate segment without special armature.

First basal segment of right fifth foot of male (Fig. 3) slightly longer than broad and bearing a tubercle at its outer distal angle which is armed with a sharp strong spine. Second basal segment three fourths as broad as long; provided with a tubercle bearing three minute spines at the inner distal angle, and the usual hair on the outer margin. First segment of the outer ramus is as broad as long and has a ridge projecting on its caudal surface near the distal end. Second segment of the outer ramus is two and one half times as long as wide and bears a small spine on its inner margin; outer margin has a long spine more than half as long as the segment, which is placed slightly beyond the beginning of its proximal third and is denticulate on its inner margin. Terminal hook about twice as long as the preceding segment, not strongly tapering; curved somewhat sharply near the center; inner margin denticulate throughout its outer three fourths. Inner ramus of right fifth foot, one-segmented; extending well beyond the end of the first segment of the outer ramus; hairy at the distal end on both margins.

Basal segment of male left fifth foot broader than long; armed with a spinous process at its outer distal angle. Second basal segment about as broad as long; provided with the usual hair, and roughened at its inner distal angle. First segment of the outer ramus longer than preceding segment; twice as long as broad; inner surface hairy. Second segment hairy on inner proximal surface; armed with a long finger-like terminal process and also with a shorter conical process on the projecting inner surface; the latter is separated from the rest of the segment by a suture. Inner ramus one-segmented; broad at base and strongly tapering; hairy on outer two thirds of inner surface and rough on basal third; about as long as first segment of outer ramus.

First basal segment of female fifth foot (Fig. 2) produced at the outer distal angle. Second basal segment triangular and bearing the usual hair on the outer margin. First segment of outer ramus almost twice as long as wide; slightly arcuate. Terminal segment about equal to the preceding in length; slightly curved; denticulate on the middle third of its inner margin; armed on the outer side with two spines, the inner of which is one third as long as the segment and the outer one somewhat less. The inner ramus is longer than the first segment of the outer ramus; acutely pointed; hairy on inner surface at the tip; armed with two spines slightly more than one half as long as the segment.

Length: female, 1.0–1.09 mm.; male, 0.97–1.0 mm.

This species strongly resembles *D. reighardi* Marsh, but differs from it in enough points to be easily distinguished. Specimens

have been examined from Arlington, Brighton, Cambridge, and Wood's Hole, which were taken in June, July, and August. It therefore seems probable that this species is common in eastern Massachusetts during the summer months.

Diaptomus spatulocrenatus n. sp.

Figs. 6–9

Description. — Cephalothorax robust and six-segmented. The first segment is three fourths the length of the cephalothorax, shows a dorsal transverse groove at about its middle. Last two segments indistinct on the dorsal surface. Last segment produced posteriorly and armed with two sharp spines on each side (Fig. 7). Abdomen stout, first segment longer than the remainder of the abdomen; second segment one sixth as long as first and one half as long as third. Furcal rami one fourth longer than wide; hairy on inner margin.

Antennæ twenty-five-segmented; those of the female extending to the tips of the furca.

Right antenna of male (Fig. 6) geniculate; swollen from the eleventh segment to the geniculate joint; twelfth segment armed with a strong pointed process which is longer than the segment is wide; ninth and tenth segments armed with shorter processes; antepenultimate segment armed with a sharp curved process which is a little over half as long as the penultimate segment.

FIG. 6. — *Diaptomus spatulocrenatus*. Right antenna, male. × 88.

FIG. 7. — *Diaptomus spatulocrenatus*. Left side of female showing end of cephalothorax. × 136.

Fifth feet of male (Fig. 8) characteristic. First basal segment of left foot reaching almost to end of first segment of outer ramus of right fifth foot; as wide as long; armed on the posterior surface with a long slender spine at the outer distal angle. Second basal segment two thirds as wide

as long, slightly tapering, the usual hair on the outer margin. First segment of outer ramus not quite half as wide as long, hairy at the inner distal angle. Second segment hairy within, armed at the outer distal angle with a strong blunt process which is minutely denticulate on its inner margin, and at the inner distal angle with a slender hair which is as long as the segment and hairy on the inner margin. Inner ramus two-segmented, reaching almost to tip of outer ramus; first segment one fifth

8

9

FIG. 8.— *Diaptomus spatulocrenatus.* Fifth feet, male. × 168.
FIG. 9.— *Diaptomus spatulocrenatus.* Right fifth foot, female. × 247.

as wide as long; second segment spatulate, crenate on inner margin, covered with minute hairs at tip and on inner and anterior surfaces. Right fifth foot of male with first basal segment armed at the distal end with a sharp spine; second basal segment armed with a large tubercle on its inner margin at the distal third and the usual hair on the outer margin. Inner ramus rudimentary being represented by a blunt curved process which does not reach beyond the end of the second basal segment. First

segment of outer ramus about as long as second basal segment, over twice as wide as long; second segment nearly twice as long as first, armed at outer distal angle with a stout hook more than one half as long as the segment. Terminal hook stout, tapering, with a sharp curve at about the middle, not quite as long as preceding segment, denticulate on inner margin beyond the sharp curve.

Fifth feet of female (Fig. 9) with the first basal segment bearing a very large pointed process at the outer distal angle; second basal segment armed with the usual marginal hair. Inner ramus one-segmented reaching beyond the first segment of outer ramus, tips hairy and armed with two plumose spines which are more than half as long as the ramus. Outer ramus two-segmented; first segment about twice as long as wide; second segment one third longer than first, curved, bluntly pointed, denticulate on outer two thirds of inner margin and armed with three spines on the outer margin of which the inner one (plumose) is longest and the outer one shortest.

Length: female, 1.47–1.58 mm.; male, 1.30–1.33 mm.

This species somewhat resembles *Diaptomus lintoni* Forbes. The specimens upon which the above description is based, were collected in Wigwam Pond, Nantucket Island, Mass., May 30, 1905, by G. D. Richmond. There were three males and two females. One of the latter was carrying eggs and both bore spermatophores.

Genus CYCLOPS O. F. Müller

Cyclops leuckarti Claus.—Localities: Cambridge, Middlesex Fells.

Cyclops edax Forbes.—Localities: Cambridge, Lexington.

Cyclops viridis insectus Forbes.—The most abundant member of this genus in the collections examined. Localities: Arlington, Cambridge, Brookline, Middlesex Fells, Nantucket, Waltham, Wood's Hole.

Cyclops viridis brevispinosus Herrick.—Localities: Cambridge, Watertown.

Cyclops vernalis Fischer.—Localities: Brookline, Arlington.

Cyclops bicuspidatus Claus.—This is a common species. Localities: Arlington, Cambridge, Middlesex Fells, Nantucket, Waltham.

Cyclops fuscus (Jurine).—Localities: Brookline, Middlesex Fells, Wellesley.

Cyclops albidus (Jurine).—An abundant species. Localities: Arlington, Brookline, Cambridge, Nantucket, Watertown, Wellesley.

Cyclops bicolor Sars.—This species was observed only once at Cambridge, on August 6, 1905.

Cyclops varicans Sars.—Occurred once in a collection made on Nantucket Island, May 30, 1905.

Cyclops serrulatus Fischer.—An abundant species. Localities: Arlington, Brookline, Cambridge, Middlesex Fells, Nantucket, Randolph, Watertown, Wellesley.

Cyclops phaleratus Koch.—Localities: Cambridge, Wellesley.

Cyclops fimbriatus poppei Rehberg.—Localities: Cambridge, Middlesex Fells, Nantucket.

Genus Canthocamptus Westwood

Canthocamptus staphylinoides Pearse.—This is an abundant species. Localities: Cambridge, Middlesex Fells, Nantucket, Reading, Wellesley.

Canthocamptus illinoisensis Forbes.—Common in a dredging made October 9, 1905, at Wellesley.

Canthocamptus minutus Claus.—Localities: Middlesex Fells, Stony Brook.

Canthocamptus northumbricus americanus Herrick.—This species occurred in a collection made October 9, 1905, at Wellesley. The length of the female was 1.16 mm. which is longer than Herrick ('95) gives. In other respects the female was similar to his figures in Plate 29. No males were taken.

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VARIATIONS IN THE POLLEN GRAIN OF *PICEA EXCELSA*[1]

JAMES B. POLLOCK

Introduction

While teaching the reproduction of gymnosperms to a class in the University of Michigan, the writer observed a very unusual structure in a pollen grain of *Picea excelsa* L. (Pl. 1, Fig. 10). The structure of this pollen grain was reported at the meeting of the Botanists of the Central States, in December, 1901, and the suggestion was made that possibly the extra cells found at the dorsal side of the pollen grain should be interpreted as a prothallium, much more highly developed than usual.

On using some of the same material for other classes it was found that the structure in question occurred rather frequently, along with other variations in the structure of the pollen grain of Picea, so that it was considered of sufficient importance to report in the present paper. As will appear later, a further examination of numerous pollen grains has led to an interpretation of the observation different from the one suggested above.

The material was a part of the stock material of the botanical laboratory at the University of Michigan, collected May 14, 1884, but there was no indication on the label as to who was the collector, where it was collected, or of the method of killing the material. The condition of the material suggested that it was killed by putting it directly into alcohol. In all the grains the protoplasm was considerably contracted from the walls of the cells, but was otherwise well preserved.

Methods

In order to make the interior structure of the pollen grains as plain as possible, the anthers, which were almost at the stage of

[1] Contribution 88 from the Botanical Department of the University of Michigan.

dehiscence, were allowed to stand in a solution of Kleinenberg's hæmatoxylin for twenty-four hours. They were then washed in alcohol and changed very gradually from 96% alcohol to pure clove oil. In the clove oil the pollen sacs were broken up and the pollen grains set free in the oil. The pollen grains were studied by mounting a drop of the oil containing them. It was found that the pollen grains stained very unequally, some not having stained at all, and others having stained so densely that the interior could not be seen. Examination showed that the unstained ones were often the most satisfactory objects for study, so no further efforts at staining were made. This is the method used in demonstrating the interior structure of the pollen grain to large classes, and the author has no claim as the originator of the method. When the grain is thoroughly permeated by the clove oil it becomes so transparent that the interior can be seen very plainly.

The contracted condition of the protoplasm of the various cells in the interior of the pollen grain made the outlines of these cells very plain, and their number easy to determine with certainty in a large series of the grains examined. Thus the crudeness of the method of killing the material proved a decided advantage in the study of it. Another advantage appeared in mounting the pollen grains in clove oil, in that the same individual pollen grain could be studied from different points of view on causing it to roll over by means of pressure on the cover glass. Two views of the same pollen grain are shown in Figs. 11 and 12, also in Figs. 13 and 14 (Pl. 1).

HISTORICAL

The older literature concerning the pollen grain has reference to the external characters and structure, and for the internal structure there is no need to go farther back than 1834, when von Mohl published his work, *Ueber den Bau und die Formen der Pollenkörner* ('34). In this article von Mohl cites the older literature on the subject, and figures pollen grains of a few gymnosperms. His figures, however, do not show internal structure, and only in the work of Fritzsche (1836), do we first find figures which show something of the internal structure of the pollen of gymnosperms as we now know it.

Among numerous species of angiosperms and a few gymnosperms Fritzsche ('36, p. 693) described and figured the pollen grains of *Pinus sylvestris* and *Pinus larix* (*Larix europæa*). The terms he used for the different cells formed in the pollen grains were totally different from those now in use. He did not regard the bodies seen as cells, nor did he have any knowledge of their function or homology. His figures show, however, a remarkable accuracy of observation, if we take into consideration the state of knowledge of his time, and the comparatively poor microscopes and crude microscopical methods. He examined the pollen grains in oil of lemon (Citronenöl), and he undoubtedly saw one of the disintegrating prothallial cells in both *Pinus sylvestris* and *Larix europæa*. His Plate 3, Figure 10, shows this for the former, and Figure 14 for the latter. In Larix, besides the disintegrating prothallial cell, he showed the cells which were later called the "stalk" and "body" cells. The latter, Fritzsche called the central vesicle, and the other two cells he called "Zwischenkörper."

Later investigations have shown that in Larix, and sometimes in Pinus also, there are two prothallial cells cut off which later may disintegrate wholly or partly. It is not safe, however, to conclude that these genera vary in the number of prothallial cells formed merely because Fritzsche did not see two of them while other writers have done so. When we remember the difficulties encountered by later observers equipped with much better microscopes than Fritzsche could have had in 1836, the wonder is that he saw so much.

Meyen ('39) pointed out that Fritzsche's "Zwischenkörper" were really cells, and that one of them served as stalk of attachment to the larger cell. This was probably the first application of the term "stalk" to this cell ('39, p. 189).

For about two decades after this time the literature concerning the pollen grain is occupied mostly with evidence for and against the view of Schleiden, advanced in 1837, that the embryo has its origin in the pollen tube. Schacht ('52, p. 407) went so far as to say that the pollen is the egg of the plants, and that there is no real analogy between animal and plant fertilization among phanerogams.

Hugo von Mohl ('55), Hofmeister ('55), and others opposed

these views, and it was only when Schacht himself discovered in *Gladiolus segetum* ('58a) a case in which the embryo undoubtedly originated in a cell which was in the embryo-sac previous to the advent of the pollen tube, that the controversy practically came to an end in favor of the views of Hofmeister and von Mohl.

Schacht ('60) reported variations in the structure of the pollen grains of several gymnosperms. On page 143 of the article designated he says that the pollen of *Cupressus sempervirens* has a slightly elongated roundish form, which has divided into two unequal cells when the anther opens. *Thuja orientalis* shows the same relation, only here *oftener than in Cupressus* (italics are mine) further division takes place in the larger cell. Two of these extra divisions are shown in his Figures 22 and 23, Plate 17. The text cited above implies that similar divisions are formed in Cupressus, but none are figured. Schacht also found variations in the number of cells in pollen grains of *Larix europæa*, shown in his Figures 4 and 5. Since Schacht did not understand that one or more of the cells first cut off in these pollen grains may disintegrate, it is possible that his observations do not really mean a variation in the total number of cells formed in Larix, but his figures seem to the writer to indicate that he actually observed such a variation in *Larix europæa*. He also states ('60, p. 144) that *Abies pectinata* (Tanne), *Picea vulgaris* (Fichte) [*Picea excelsa* L.], and *Pinus sylvestris* (Kiefer) are like Larix in the interior of the pollen grain, only in the first two there are almost always three cells, and in the latter sometimes only two. No figures are given for these, but it seems probable that Schacht really observed variations in the number of cells in the pollen of the species named. Schacht was probably the first to figure the sperm cells ('58a) though he did not understand their function.

Hofmeister ('62, p. 406) described the structure in the pollen of Juniperus, Taxus, and Thuja differently from what it is now understood to be, but the apparent variation is probably due to a wrong interpretation.

Juranyi in a preliminary notice in 1870 and in the fuller article in 1872, reported a variation in the number of cells found in the pollen of *Ceratozamia longifolia* Miq. He found that the one-celled stage of the pollen grain divided into a large and a small

cell, the latter bulging into the former. The smaller cell divides again into two unequal cells, the smaller lying against the pollen grain wall, the larger one being hemispherical. Most pollen grains are ripe at this stage of development, and undergo no further changes till the time of fertilization. Often, however, one meets a pollen grain which does not remain at this stage of development, but goes a step farther in that the hemispherical cell divides once more, so that a three-celled body is found in the interior of the pollen grain. Juranyi's Figures 3 and 8 of Plate 33 ('72) show very well what he found. He, as well as Hofmeister, was mistaken as to the divisions of the smaller cells, since later investigations have shown that the small cells are cut off successively from the larger one and that only the last of the smaller cells divides when the "stalk" and "body or central" cells are formed. Juranyi's figure ('72, Pl. 33, Fig. 8), which shows three small cells, may either be an actual variation in the number of cells, or it may be a case of premature division into "stalk" and "central" cells. No certain conclusion can be reached, but if the division into "stalk" and "central" cells is the same in Ceratozamia as Webber found in Zamia, then Juranyi's figures of the former do indicate a variation in the number of prothallial cells or else a two-celled stalk. In 1882, Juranyi reported that he had seen a few cases among the Cycadaceæ in which the small cells could divide parallel to the long axis of the prothallium (Vorkeim), and that in *Larix europæa* he found some pollen grains in which the prothallium ended with two cells lying beside each other, and separated by a division wall. The upper cell had divided parallel to the long axis of the prothallium. In the cases just mentioned in which the small cells in some of the Cycadaceæ divide parallel to the long axis of the prothallium, it cannot be questioned that we have a case of variation from the normal, both as to the number of cells formed, and as to the relation of those cells to each other in space. In the cases of *Larix europæa* in the upper cell there may have been an earlier division than usual into the two sperm cells, though at the time these observations were made the exact origin of the sperm cells was not understood.

Strasburger, in *Die Coniferen und Gnetaceen* ('72) added much to our knowledge of these plants, though some of his observations

were inaccurate and his earlier conclusions wrong. Strasburger wrongly interpreted the disintegrating cells at the base of the pollen grain as mere slits in the wall having an origin similar to that of the wings of the grain ('72, p. 127). Schacht ('60) had interpreted these correctly as also had Meyen ('39). Following Hofmeister's suggestion Strasburger said that the cells formed in the interior of the pollen grain could only be considered vegetative cells, homologous to the prothallium of the fern. He supposed the large cell of the pollen grain corresponded to an antheridium, believing that it furnished the male gametes. He also thought that the cell structure was the same in Pinus, Podocarpus, and Cupressus ('72, p. 130). Later investigations have shown that no two of these are *exactly* alike. On page 131 Strasburger ('72) remarks that the number of cells which are formed by division in the pollen grain in Cycads and Coniferæ remains constant. It never exceeds two, according to his observations. The report of a larger number can only be founded on the view that the split in the wall is a disintegrated cell.

In a paper published in 1875, Tschistiakoff wrote that where there are several small cells, they arise *by successive division of the large pollen cell* as in Larix, or the second cell can divide to form two cells as in Ginkgo ('75, p. 100). In Pinus according to Tschistiakoff two, or at the most three small cells arise. The one or two first cells arise by a real division of the large pollen cell. The small cells may have their whole volume in the intine. The third large cell, arching into the pollen grain, arises by division of a small cell. In Abies the third cell forms by free cell formation, this divides into two, each of these can divide again, and these secondary cells can divide longitudinally or transversely. The small cells (Suspensorzellen) can likewise divide.

Though some of the observations made by Tschistiakoff were inaccurate, at least two new truths were presented, even if they were not proved, namely, that several small cells were cut off successively from the large pollen cell in such grains as those of Larix and Pinus, and that the last one of the row of cells formed, became the progenitor of spermatozoid mother cells. His article also mentions variations in the prothallium of Abies, and in the number of cells formed in Thuja, where he says there may be two divisions instead of one, and these may be in different directions.

Both of the two truths presented by Tschistiakoff were either denied or ignored by later writers, (Strasburger, '78; '80). While Juranyi ('82) admitted Tschistiakoff's view of the origin of the small cells, proving it in Cycads, and believing it true for Coniferæ, both Juranyi and Strasburger believed the large tube cell of the pollen grain furnished the male gametes and therefore represented an antheridium, and it was not until Belajeff ('91–'93) proved the contrary for *Taxus baccata* that the correct view was finally established, and generally accepted. Both Belajeff ('91–'93) and Strasburger ('92) showed that in the Abietineæ also it was not the tube cell, but the end cell of the row of interior cells formed, from which the male gametes were derived. Strasburger ('84) had previously admitted that Tschistiakoff's view of the origin of the small cells in the pollen was correct, and he had also shown that in *Larix europæa* the third small cell cut off from the large pollen cell divided into two cells which he named the "stalk" (see Meyen, '39, p. 189) and "body" cells respectively. The recognition of the "splits" in the wall of Larix pollen as disintegrating cells ('84, pp. 2–3) was a confirmation of the earlier views of Schacht and Meyen.

Strasburger ('92) reported some interesting variations in the number and arrangement of cells in the pollen of *Ginkgo biloba*. Ordinarily there are three narrow cells and one large one found in the ripe pollen grain. Usually the first two of the former are disorganized, but it often happens that two prothallium cells are absorbed and yet two permanent ones are found. Also pollen grains were repeatedly observed in which there were three permanent inner cells preceded by one absorbed cell. Finally one grain was seen in which all three prothallium cells were permanent, and the first of these was divided longitudinally. Also (Strasburger, '92, p. 18) the stalk cell of the antheridium appears to divide under some circumstances.

Since 1893 the most important step in the progress of our knowledge of the pollen of gymnosperms was the discovery of motile spermatozoids in 1896 and 1897, by Ikeno ('98) in Cycas, by Hirase ('97) in Ginkgo, and by Webber ('97) in Zamia. Webber's (:01) observations on Zamia and Ginkgo are interesting from the point of view of variation in those genera. He did not work out

the details of the formation of prothallial cells, but in the species of Zamia studied there were always at least two prothallial cells cut off at one side and projecting into the grain as in Ceratozamia and Macrozamia, and different from Cycas and Ginkgo, where the walls are straight across the grain and not arching into it. It seemed to Webber, however, that three prothallial cells were occasionally formed, and in this case the first one was resorbed as described by Strasburger and others in Pinus, Ginkgo, etc., remaining as a dark refractive layer in the wall of the pollen grain, situated at the point of contact of the other cells. In many instances in mature grains, and in later stages, during germination, no indication of this resorbed prothallial cell can be observed, but in some cases it is unmistakable. A careful investigation of the development of the pollen in Zamia will have to be made before it can be determined whether three prothallial cells are regularly formed or whether the remnants of a third cell, occasionally observed, are to be considered as cases of rare and somewhat abnormal development.

Webber (:01, p. 24) clears up a point in the origin of the stalk cell and the central cell (body cell of Strasburger) showing that they originate by the division of the inner prothallial cell. Up to the time of Webber's full publication this point was quite obscure and this brings it in agreement with the facts in other gymnosperms investigated, except that the sterile cell bulges strongly into the stalk cell and this had led to a wrong interpretation. Webber also shows that Ginkgo is *probably* similar to Zamia on this point, and Seward and Gowan (:00, p. 130) show that this is actually the case. They also state that in Ginkgo the pollen grain at maturity contains a prothallium of from 3 to 5 cells.

Lang ('97) reports that *Stangeria paradoxa* has two prothallial cells when pollen is shed, but his Figure 18, Plate 22, seems to show three.

An interesting question is suggested by the different results observed in two species of the genus Ephedra. Jaccard ('93) reported that in *E. helvetica* at the time of anthesis there were in the pollen grain three free nuclei, but not separate cells, and he called these nuclei respectively the prothallium nucleus, the generative nucleus, and the tube nucleus. Land (:04) in *Ephedra*

trifurca found two persistent prothallial cells, the first cut off by a wall, the second not so cut off, while a third cell which he calls the primary spermatogenous cell divides into the stalk and body cells, which are not separated by a wall, but have a common membrane (not cellulose but plasmic?). At time of anthesis therefore it has two prothallial cells, a stalk cell, a body cell, and a tube nucleus. Land (:04, p. 8) remarks that it is hardly to be expected that two prothallial cells will be present in one species and wholly absent in another of the same genus. The question, however, cannot be settled in this summary manner. Jaccard's observations can be set aside only after further examination of the same species he studied, and not by the examination of another species.

Miss Ferguson (:01, Pl. 12, Fig. 6) figures pollen grains of *Pinus strobus* with two prothallial cells, and also with one prothallial cell (Pl. 12, Fig. 8), and in the latter case she labels the one cell shown as the *second* prothallial cell. Of course this is on the supposition that the same number of cells is always produced in this species, and that in the pollen grain shown in her Figure 8 the first cell formed had disappeared. The question naturally arises, however, whether this may not be a real variation, and the prothallial cell shown, be the only one formed in this case. A decisive answer of course must rest on further observations.

Coker (:02) has described some interesting variations in Podocarpus. The two prothallial cells do not promptly disintegrate, but persist as cells, and the second, and sometimes the first also, behaves in a manner hitherto unknown among the Conifers, and only paralleled among the Cycads and in Ginkgo. The nuclei enlarge and become as conspicuous as the generative nucleus. The cytoplasm of the second prothallial cell loses its individuality and its nucleus slips from its former position and lies free in the general cytoplasm. This nucleus may divide amitotically before liberation. In such cases the two nuclei generally slip out in different directions and place themselves on opposite sides of the generative cell (Coker, :02, Pl. 5, Figs. 8, 10). The number of cases in which this division occurs is probably as great as the number in which it does not occur. Hundreds of cases were found. In not a few cases the first prothallial cell liberates its nucleus into the general cytoplasm.

Arnoldi (:00) has reported a variation somewhat similar to this in *Cephalotaxus fortunei*, where he found the *tube nucleus* dividing amitotically, thus showing three free nuclei in the end of the pollen tube besides the generative cells. Arnoldi actually observed one case of division of the tube nucleus. He also reports that the non-functional male nucleus may divide amitotically in the upper part of the egg. Two tube nuclei were reported by Juranyi ('72, Pl. 34, Figs. 11, 12) in Ceratozamia. Two or more tube nuclei have been reported in the angiosperms, (Chamberlain, '97; Fullmer, '99; Smith, '98). The last-named author found two tube nuclei in half the pollen grains examined in *Eichhornia crassipes*.

Juel (:04) has found in Cupressus a variation which he seems to have discovered for the first time among the gymnosperms. In the pollen tube of this genus he found not merely two sperms, but from eight to ten, or even twenty in some cases. Chamberlain ('97) had found in angiosperms occasionally a pollen grain with three sperm nuclei. In the same species, *Lilium philadelphicum*, he also found a number of cases of a prothallial cell cut off at one side of the pollen grain.

Thompson (:05) has reported that in the pollen tube of Araucaria and Agathis there are supernumerary nuclei. His preliminary note did not disclose their origin.

Lopriori (:05) shows that in *Araucaria bidwellii* these supernumerary nuclei arise from cells formed in the pollen grain, primarily by unequal division of the large cell of the pollen grain, and the smaller cells thus cut off may themselves divide until there are fifteen or more. These cells at first have walls but the walls dissolve and the nuclei come to lie free in the pollen tube. Lopriori believes these cells are spermatogenous cells and the nuclei derived from them male nuclei. The writer does not accept this interpretation of Lopriori and will give reasons for his opinion in connection with a later discussion.

Miyake (:03) found in *Abies balsamea* that the second sperm nucleus, the tube nucleus, and the stalk nucleus which are left in the upper part of the egg after fertilization, may all divide, or attempt to divide, before they disintegrate. He says that the division figures are more or less abortive or abnormal, hence the divisions are apparently mitotic ones. This author saw one case

of "double fertilization," in which the second sperm nucleus united with a secondary segmentation nucleus of the fertilized egg.

If one could always rely on the observations reported in the literature, the conclusion would have to be drawn that in other gymnosperms than Cupressus and possibly the Araucarineæ there were variations in the number of male cells. Tschistiakoff supposed that there might be numerous spermatozoid mother cells formed and Strasburger ('80, p. 49) writing of *Juniperus virginiana* states that one of the two primordial cells found at the tip of the pollen tube, divides into two, and often into two more, and these are used for fertilization. At a later date, however, the same author states ('92, p. 32) that in all the cases he has had opportunity to study exactly, the generative (primordial) cell of gymnosperms divides into two sister cells. Both are generative and even in the Cupressineæ both are called to perform a sexual function (p. 33). In the Abietineæ a difference in size between the cells makes its appearance, and finally in Taxus a very unequal division of the generative cell takes place, and only the larger sister cell functions in fertilization. Since that statement was written by Strasburger, numerous writers all report only two male cells from each pollen grain, and we must conclude that the earlier observations were not correct as to the larger number; so that Cupressus stands alone among the gymnosperms in forming numerous sperm cells, unless the supernumerary nuclei reported in the pollen tube of Araucarineæ by Thompson (:05) and Lopriori should prove to be sperm cells, as Lopriori believes or else this variation among the gymnosperms has been generally overlooked. The variation in the *size* of the male cells formed is common.

In a recent work on the gymnosperms, in fact the only one in which an adequate discussion of the group is given from the modern point of view (Coulter and Chamberlain, :03) a variation is noted in the Cycadaceæ and Ginkgo, as compared with other gymnosperms, in the relative position of the "stalk" and "body" cells. They are said to stand side by side, instead of dorsiventrally as they do in the other gymnosperms. These descriptions (pp. 25, 42) are evidently based on the descriptions and figures of Hirase for Ginkgo, and of Ikeno for Cycas. If Webber's completed

work on Zamia (:01) had appeared somewhat sooner the descriptions as to Ginkgo would necessarily have been different in the above-mentioned work. Webber shows very conclusively that in Zamia, and in all probability in Ginkgo also, the division into stalk and central cell (body cell) does not leave those cells side by side, but in the position found in the other groups of gymnosperms. The bulging of the last vegetative prothallial cell into the stalk cell probably led to a wrong interpretation of the earlier observations. Webber pointed out that the work of Ikeno and Hirase was obscure on this point, and that before it can be certainly concluded that any Cycad divides so as to bring the stalk and body cell side by side, except as an unusual variation, the figures showing the stages of development must be more convincing than those now available.

Lawson (:04) found a variation in the behavior of the nuclei and cells in the pollen grain of *Cryptomeria japonica*, as compared with other gymnosperms which have the same number of nuclei. The primary spermatogenous nucleus is free in the cytoplasm of the pollen grain and not separated from the tube nucleus by any membrane, except for a short time, and even then the membrane is so difficult to distinguish that it almost escaped the observation of the author.

Variations in the pollen grain of several gymnosperms have been reported in the *Botanical Gazette* by Coker (:04a) one of which is much like some of those found in *Picea excelsa* by the present writer. Coker's Figure 7 of *Larix europæa* is similar to my Figure 8. His Figure 6 is merely an earlier stage of the same thing. His Figure 8 of *Larix europæa* and Figure 4 of *Cupressus sempervirens* show a condition that is like that found by Lawson in *Cryptomeria japonica*. Coker's Figure 9 of *Larix europæa* shows the last division wall in the pollen grain straight across, as is usual in Cycas, instead of the strongly bulging wall that is usual in Larix.

Coker merely reports these as abnormal grains, apparently not attaching any significance to them. It seems to the writer that they are of some significance, at least as indicating the limits of variation in the different genera and species of gymnosperms, and when our knowledge of these variations is more complete they may be of some assistance in determining whether or not the struc-

ture of the pollen grain in gymnosperms is at the present time in a state of stable equilibrium or in a process of retrogressive modification. Coker's Figures 6 and 7 will be further noticed in connection with some of mine.

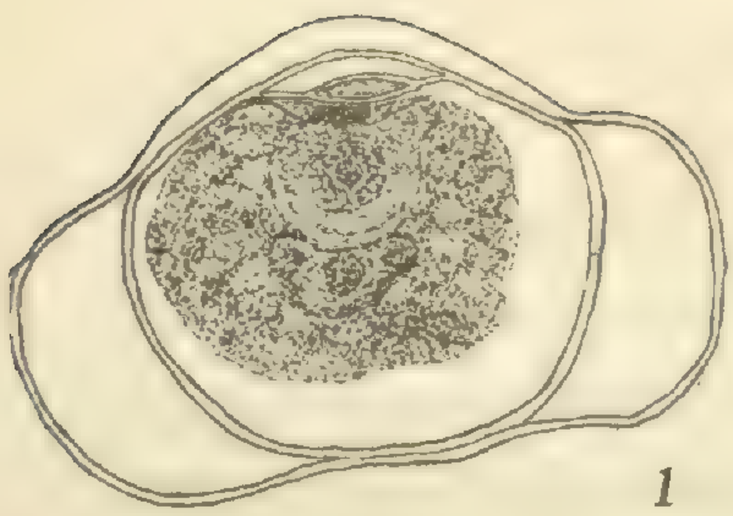
Picea excelsa

In presenting my own observations I have considered it desirable to illustrate rather fully the different variations found in the pollen grains of *Picea excelsa* L., and these illustrations show a surprising range in the variation in internal structure of the pollen. One fact that seemed especially significant was that so few pollen grains could be found showing satisfactorily what has been called the "normal" structure, that is showing *two* disintegrating prothallial cells. For the larger number of pollen grains showed only one such disintegrating cell without a trace of a second, even as a split in the wall of the pollen grain. In order to get at the proportion of those which showed only one disintegrating prothallial cell, 466 pollen grains were counted. Only those were counted which lay in the position most favorable to the necessary observation, that is, the side view as shown in Figs. 1–6 (Pl. 1). No pollen grain was counted unless its internal structure seemed reasonably clear. Of the total of 466 grains counted, 310 or 66.5% showed only one disintegrating prothallial cell with no trace of another even as a split in the wall; 73 or 15.7% showed more or less plainly two disintegrating prothallial cells; 18 or 3.8% showed no disintegrating cells; 65 or 13.9% were doubtful as to whether they had one or two disintegrating cells. Even if all the doubtful ones are counted as "normal" the percentage of those grains which showed only one prothallial cell is still more than twice as great as the "normal." Of course it may be said that in those grains in which only one prothallial cell showed, the one first formed had completely disappeared. But if it is not to be seen, what evidence is there that it was ever formed? Two reasons may perhaps be given for believing in its formation and disappearance. First, in many cases in which two prothallial cells may be recognized the one first formed is barely recognizable as a mere slit in the wall of the pollen grain, and it is probable that in some cases the cell

disappears so completely as not to be recognizable at all. Second, it is said that the pollen grain of Picea always forms "normally" two prothallial cells which disintegrate more or less, hence when only one is found the other must have disappeared. Some validity must of course be granted to the first reason given. It is probably true in some cases, but it is absolutely impossible to prove its truth in a given case, hence the number of cases in which it is true is purely a matter of conjecture. As to the second reason given, it is a conclusion based on observation, and cannot be used to prove the correctness of the observations upon which it rests. Back of it lies the assumption that the "normal" is invariable, an assumption which is far from the truth. Even if some pollen grains of Picea have been shown to form two disintegrating prothallial cells, it does not at all follow that they do so invariably.

Fig. 4 (Pl. 1) shows a pollen grain in which there were undoubtedly *three* disintegrating prothallial cells. All of them were persistent, and separate from each other, and from the antheridium part of the pollen grain, so that there was no difficulty in recognizing the number certainly. This grain was at the stage preceding the division which separates the stalk and the central cell. The third disintegrating cell cannot be interpreted as a stalk cell, first, because it so closely resembles the other disintegrating prothallial cells in size and appearance, and second, because it is so completely separated from the dome-shaped cell to which it would be closely attached if it were a stalk cell.

Fig. 5 (Pl. 1) shows a variation in the *position* of the prothallial cells, though their *number* is "normal," that is, two. In Fig. 6 (Pl. 1) there is a variation in both the number and the position. Three pollen grains were seen like Fig. 5, but only one like Fig. 6. The latter shows without any doubt whatever a case of three prothallial cells in addition to the stalk cell, central cell, and large cell that forms the pollen tube. If Fig. 4 has been correctly interpreted, it and Fig. 6 furnish direct proof that the number of prothallial cells in Picea may vary from what has been called the normal in the direction of a greater number and it seems much more probable that they would also vary in the direction of a smaller number, since so many of the gymnosperms, as Thuja and Juniperus, have no vegetative prothallial cell.



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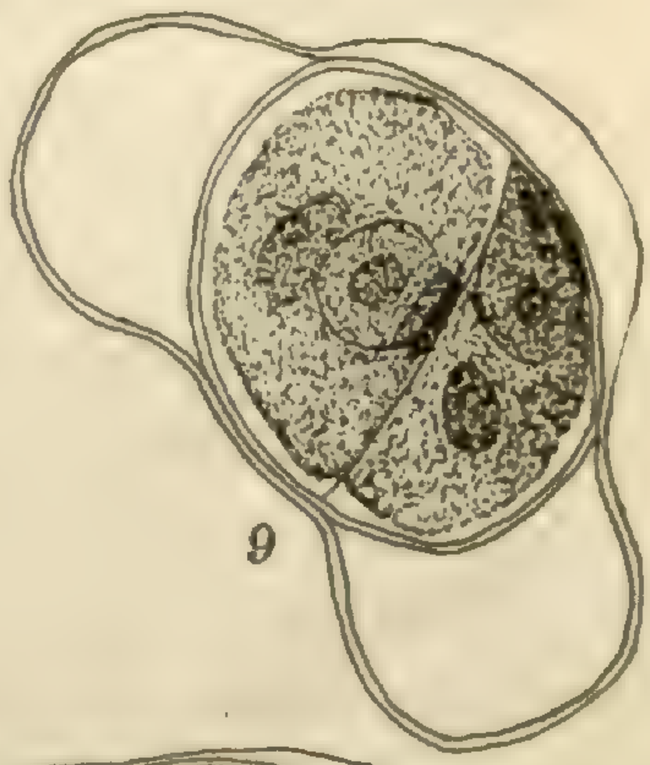

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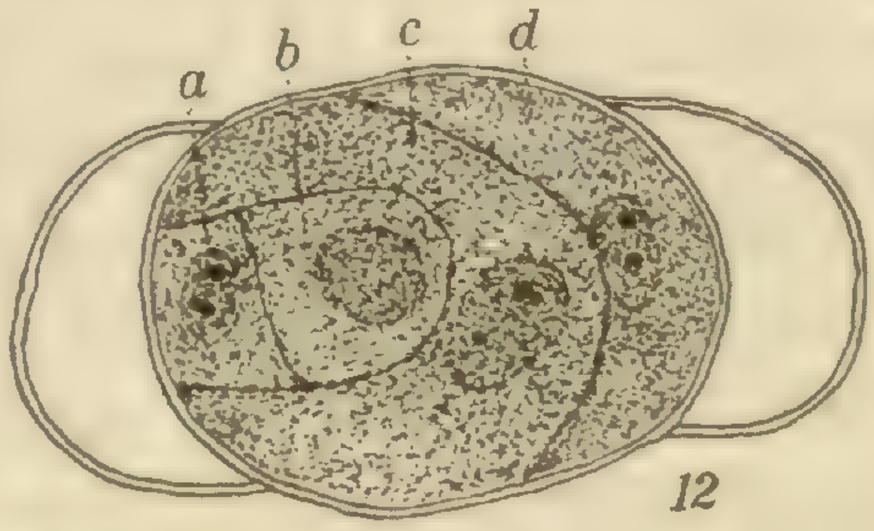

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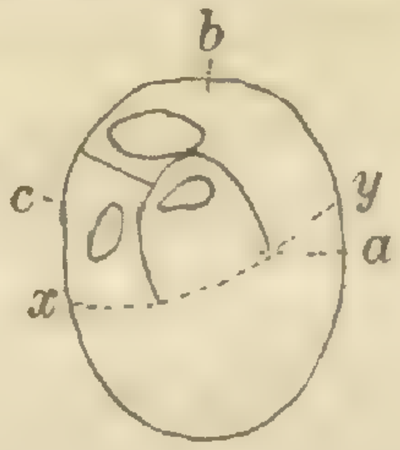

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PLATE I.

Picea excelsa, variation in the pollen grains.

Fig. 2 (Pl. 1) also seems to show three prothallial cells, one with no protoplasm, and two with very little. In this case the walls of the cells had persisted after the protoplasm had almost or entirely disappeared, and so far as appearance was concerned seemed to be like the inner layer of the pollen grain wall and continuous with it. Usually, however, these cells do not show so persistent and evident a membrane. Fig. 1 has the number regarded as the normal for Picea. In this case also the membrane persisted after the protoplasm was entirely gone in the first one formed, showing that the membranes were not plasmic, but in all probability of cellulose. No microchemical tests were made on them. Fig. 1 shows a distinct separation of the protoplasm of the central cell from that of the large tube cell. This separation was the result of plasmolysis, probably due to the killing fluid. The boundary of this cell, however, appeared to be only a plasmic membrane. At least it was exceedingly thin and closely applied to the surface of the protoplasm.

Fig. 3 (Pl. 1) shows the typical arrangement of cells, with two prothallial cells, but between the main part of the pollen grain and the wings there are two spaces cut off by cellulose walls, containing no trace of protoplasm. The writer was unable to decide whether these should be considered as cells or not. They seemed to bear no definite relation to the main part of the pollen grain. In this grain the membrane surrounding the central cell, and continued around the stalk cell, plainly projected beyond the limits of the protoplasm where it had been pulled away from the wall of the pollen grain by plasmolysis. This membrane was very much thinner than the inner cellulose layer of the wall of the pollen grain, but if it was only a plasmic membrane it was at least much firmer than the protoplasm which it bounded, and from which it was partly separated by plasmolysis.

There is shown in Fig. 7 (Pl. 1) a variation somewhat different from those already discussed. Only one disintegrating prothallial cell is apparent, but projecting into the tube cell of the pollen grain is a row of three cells of approximately equal size and structure except that the innermost one of the row is dome-shaped while the others are flattened against the adjacent cells. These three cells have equally large, prominent, and well preserved

nuclei, and apparently either the stalk cell or the central cell of the typical pollen grain has in this case divided again. There was no indication as to which of the two furnished the third cell found here. Another interpretation of this pollen grain is possible. The outermost of the three almost equal cells might be regarded as the second prothallial cell. The writer does not accept this interpretation of that cell because of its large size, its prominent and well preserved nucleus, and its close connection with and general resemblance to the adjacent cell.

A very different type of variation is illustrated in Fig. 8 (Pl. 1). Here the pollen grain, while having the typical form externally, is divided into two equal portions by a wall perpendicular to the long axis of the grain. This wall was very plain where it joined the outer wall of the grain, but where the protoplasm lay against it on both sides it could not be recognized certainly, and it was represented in the drawing only where is was unmistakable. Its position is probably indicated by the cleft in the protoplasm which throws five cells on one side and three on the other. This gives the typical form and arrangement of cells with two prothallial cells on one side, while on the other side of the dividing wall no prothallial cells are formed, and the three cells present apparently represent a stalk cell, a central cell, and a tube cell. The writer believes this difference in the two halves to be of some importance in relation to the variation in number of prothallial cells. If the number of those that disintegrate is invariably two for each pollen grain, which ordinarily has one antheridium, in this double grain where there are two antheridia, there ought to be two disintegrating cells for each antheridium. If it be supposed that one set of two prothallial cells serves as the basis of two antheridia, variation from this arrangement and number of prothallial cells is found in other grains of this same type, containing two antheridia. Fig. 9 shows a grain with the two antheridia in different positions in their respective portions, and each has only one disintegrating prothallial cell visible. Thirty-two grains of this double type were studied in more or less detail. In most of them the two antheridia were placed as in Fig. 8. There was much variation in the number of the prothallial cells connected to the various antheridia. Put in the simplest form and using the single antheridium

instead of the double pollen grain as the basis of comparison the following table shows the amount of variation.

	2 Pr. Cells	1 Pr. Cells	No Pr. Cells	Cells Uncertain	Total Antheridia	Total No. Pollen Grains
No. of antheridia	4	24	18	18	64	32

In the group marked uncertain, the uncertainty was sometimes due to inability to recognize clearly the total number of cells present, and in other cases the position of the wall dividing the pollen grain was uncertain where it ran between the disintegrating prothallial cells. Only one sixteenth of this lot of antheridia shows what has been called the normal number of prothallial cells. Of even more importance than this fact is the further one that in no case did both the antheridia in the same double grain have two prothallial cells, as should have been the case if two is the normal number. There were several cases in which the numbers for the two antheridia were respectively 2 and 1, 2 and 0, 1 and 1, 1 and 0, 0 and 0. In those cases in which there were two prothallial cells in one part, and one or none in the other part of the double grain, it cannot be argued that some had disappeared by disintegration, because the two parts of a double grain are usually at about the same stage of development, and there is no reason to suppose that two cells should so completely disappear in one part, and none in the other. At least some cases should have been found in which both parts of the double grain had two prothallial cells, and most of the double grains should have shown the same number of prothallial cells on the two sides of the dividing wall. Since neither of these conditions was found to exist in the grains examined, and in the light of other facts reported in earlier paragraphs of this article, the writer feels justified in drawing the following conclusions: —

1. The number of disintegrating prothallial cells in the pollen grain of *Picea excelsa* L. is not invariably two, and when a grain is found which shows only one such cell it is not necessarily the *second* prothallial cell and should not be so named. At the most it can only be said that it is uncertain whether the case is one in which a prothallial cell has completely disappeared, or whether it is a case of *normal variation.*

2. The number of vegetative prothallial cells certainly varies from one to three, though the latter number is rare. It may also happen that there are none at all. This condition is comparable with that found in those gymnosperms which typically produce no prothallial cell, as Juniperus, Taxus, and others. In Picea it was found in 3.8 % of the pollen grains that contained only one antheridium.

3. The prothallial cells may vary in position as well as in number. The usual arrangement is dorsiventral, forming a single continuous row with the stalk and central cells, but two prothallial cells may be placed laterally in relation to each other instead of dorsiventrally, and in case of three cells the arrangement may be partly lateral and partly dorsiventral (Pl. 1, Figs. 5, 6).

4. In very rare cases the variation in number may extend to that part of the row of cells which usually is composed of the stalk cell and the central cell. An extra cell may be formed at this point perhaps by division from the central cell. The stalk is then two cells high.

5. The number of prothallial cells formed in the majority of pollen grains would seem to be *one*, if the results obtained in counting are to be fully relied upon, since 66.5 % of them showed but one prothallial cell as against 15.7 % which showed two. This difference is probably greater than it should be, since it cannot be denied that one cell *may* have disappeared in some of those grains which showed only one.

6. The membranes of the prothallial cells sometimes persist after the complete disappearance of the protoplasm, hence they cannot be plasmic, but are probably cellulose. In other cases there is no trace of cellulose walls.

Coker (:04a) interpreted his double pollen grains of Larix shown in his Figures 6 and 7, as having been formed by one instead of two divisions of the pollen mother-cell, and the daughter cells having been retained within the mother-cell wall. In the pollen grains of Picea studied by the writer this interpretation seems very improbable, first, because no trace of the mother-cell wall was observed around the pollen grain; second, because of the fact that the "wings" of the pollen grain were always present, and always typical in number and arrangement. If these double grains were

contained in a pollen mother-cell, the pollen mother-cell wall was cuticularized and expanded into two wings. No indications of this condition were observed.

A pollen grain with a very different appearance from that of any yet described is represented in Fig. 10 (Pl. 1), which is a drawing of the pollen grain whose discovery led to the observations recorded in this article. In this grain we have the typical tube cell, central cell, stalk cell, and what seem to be two disintegrating prothallial cells, but in addition we find lying along the dorsal wall of the pollen grain a row of four rather prominent cells, each with a nucleus. These cells appear to be of unequal size and of somewhat different shapes. They are separated from the rest of the pollen grain by a wall which was continuous with the inner layer of the wall of the grain, and which appeared just like it in structure. The presence of this wall was made evident by the contracted state of the protoplasm adjacent to it.

The structure of this grain was reported at the meeting of botanists mentioned above, and it was suggested that possibly the four cells represented a prothallium or gametophyte of a much larger size than usual, and the pollen grain showed a reversion to an earlier type of structure. At that time the writer saw no way of determining definitely whether that was the correct interpretation of the structure discovered. In succeeding years, it was found that the class material from which that pollen grain came also contained numerous others similar to it as well as the variations of the different kinds that are reported in this article.

After studying a number of grains of this same type the thought occurred that perhaps a clue to the meaning of the unusual structure might be obtained if the same grains could be studied from the dorsal as well as from the lateral view. Since the pollen grains were mounted in clove oil, this could be done, by causing them to roll over while observing them under the microscope. By repeated trials it was found possible to study some of these abnormal grains from all possible points of view, dorsal, ventral, lateral, and end views. The dorsal and lateral views were the most important.

A total of 22 grains of this structure was studied, and many of them were drawn in two or more views for purposes of comparison. Figs. 11 and 12 (Pl. 1) are respectively the lateral and dorsal

views of the same pollen grain, and Figs. 13 and 14 (Pl. 1) are the corresponding views of another grain. A study of the structure shown in Figs. 12 and 14 as well as others more or less similar to them finally suggested what the writer believes is the correct interpretation of the extra cells along the dorsal wall of pollen grains as shown in Figs. 10, 11, and 13. In Fig. 12 it will be noticed at once that the cells labeled *a* and *b* are like the stalk and central cell in a typical pollen grain, while cell *c* has the same relation to the others as a tube cell, and cell *d* has no corresponding part in the typical pollen grain. No cells appear to correspond to the prothallial cells in the typical grain. In Fig. 14 the correspondence to the typical pollen grain is less clear than in Fig. 12. Nevertheless there is a distinct suggestion of a similar structure. In short, a study of the dorsal view of as many of these grains as possible led to the conclusion that grains of this type are not so very different from the type shown in Fig. 8. They are double pollen grains, but the division wall, instead of running from dorsal to ventral side and dividing the grain into two equal parts, divides it into two very *unequal* parts, *and cuts off the smaller portion along the dorsal wall.* This interpretation was made more certain on looking over all the rough drawings made during the study, when it was found that there was a very complete series of transitional stages between the structure shown in Fig. 8 and that in Fig. 12. In these transitional stages the division wall ran from some point on the dorsal side obliquely toward one of the wings. Fig. 9 is an example of one of these transitional stages, and Fig. 15 is a diagram of what was seen in a dorsal view of a pollen grain with an oblique division wall. The dotted line *xy* is presumably the line of junction of the oblique division wall with the dorsal wall of the grain. This was of course not plain, owing to the oblique position of the receding wall. Cell *a* bulges into cells *b* and *c* like the cell which divides to form the stalk and central cell. Cells *b* and *c* taken together represent the tube cell. If, as is generally supposed, the tube cell represents an antheridium wall, then we have here a case where the antheridium wall is two-celled, a very unusual thing among the gymnosperms. One other case was observed almost exactly like this one, except for a slightly different position of the wall separating cells *b* and *c*. It is just possible that the two tube

nuclei found by Juranyi ('72) in the young pollen tube of *Ceratozamia longifolia* and by Arnoldi (:00) in *Cephalotaxus fortunei* represent two cells in the antheridium wall or tube cell of the pollen grain, but that interpretation can hardly be insisted upon very strongly on the evidence now available.

In the case of the two or more tube nuclei in the pollen tube of angiosperms, the above interpretation ought to be considered, but here there will be even more hesitation over its acceptance than in the gymnosperms.

As regards the large number of nuclei found in the pollen tube of Agathis and Araucaria, Lopriori concludes that in *Araucaria bidwellii* they are male nuclei, and that the cell-complex which is formed in the pollen tube, and from which they are derived, is a spermatogenous cell-complex. Lopriori's conclusion is evidently much influenced by Juel's discovery of the numerous male cells in Cupressus. The present writer cannot accept Lopriori's conclusion until there is direct evidence that the nuclei in question do actually function in fertilization. The reasons for rejecting the conclusion at the present time are these: —

1. The cell-complex from which the nuclei are derived is formed in the pollen grain and not in the pollen tube as Juel found in *Cupressus goweniana*.

2. It is formed, not from a single generative cell, but primarily by the successive unequal divisions of the large cell of the pollen grain, though secondarily the small cells thus formed may themselves divide in different directions.

These reasons seem sufficient to show that the cell-complex is not spermatogenous in its nature, but that it is the vegetative part of a male gametophyte, and as such is exactly the condition which the present writer thought he had found when he first saw the pollen grain of Picea represented in Fig. 10 (Pl. 1). Though this interpretation proved to be wrong for Picea, Thompson and Lopriori have probably discovered in the Araucarineæ a group of gymnosperms which have the multicellular male gametophyte, and in this particular at least they show the most primitive condition of any of the gymnosperms.

It is to be hoped that these investigators will follow out the full life history of all the cells and nuclei found in the pollen grain and tube of the Araucarineæ.

In a recent short review of Lopriori's paper, C. J. Chamberlain also rejects that writer's conclusion that the numerous nuclei are male nuclei, but he gives no reasons therefor except "judging by his figures."

The structure in Fig. 16 (Pl. 1) requires little discussion. It represents one of the somewhat irregular variations in a double grain, but the portion marked *a* seems to consist of a mass of protoplasm completely cut off from the rest, and contains no trace of a nucleus. In order to determine the frequency with which the variation of the double pollen grain occurred, a count was undertaken. Fresh drops of clove oil containing the pollen grains were mounted and all the grains on the slide were systematically counted. A separate list was made of all the grains that were double, both those like Fig. 10 and like Fig. 8 and also the ones intermediate between these two. The total number counted was 1120. Of these there were 27, or 2.4 % which showed the double character more or less plainly. This was a much higher percentage than was expected, but there is no reason to think a mistake was made in the counting. Indeed it is more probable that some of the double grains may have been overlooked. If any of them lay in the position with the dorsal or ventral side toward the observer they would almost certainly have been overlooked since in that position their double nature is very difficult to recognize. The proportion among those that were counted did not impress the observer as being any greater than the proportion among the hundreds that were not counted but were looked over in making the study of the variations found.

As a result of the study of the type of variation shown in Figs. 10–14, the following additional conclusions may be drawn: —

1. The three or four cells lying along the dorsal side of the pollen grain of this type do not constitute a prothallium or gametophyte of unusual size, an interpretation which the writer at one time thought a possibility.

2. They constitute the smaller portion of a pollen grain separated by a division wall into two very unequal portions, each of which may form a more or less typical antheridium.

3. The cells of the larger part of such a pollen grain are similar to the cells in a typical single pollen grain, and cases were observed in which the number of prothallial cells visible was 2, 1, and 0.

4. In the smaller portion of such a double pollen grain there is more variation in the size, number, and arrangement of cells, but generally there is a distinct resemblance to the typical antheridium. In several cases the similarity was striking and unmistakable.

5. In two cases where a cell which is like the one that divides into the stalk and central cell, was plainly marked, the rest of that portion of the pollen grain, which corresponds to the tube cell or antheridium wall, was divided into two cells by an anticlinal wall, that is, the antheridium wall was two celled (Pl. 1, Fig. 15).

6. In the material examined the proportion of double pollen grains was found to be 2.4 % in a count of 1120.

Writers who feel justified in labeling a single prothallial cell as the *second* one, may be inclined to reject some of the conclusions reached in this article, especially the conclusion that a majority of pollen grains in *Picea excelsa* form only one prothallial cell (p. 271) on the ground that so much of the material studied was abnormal. It has already been admitted that there is room for argument as to the *number* of pollen grains in which only one prothallial cell is formed, and the point at issue is really the determination of what is the normal number, or to state it more clearly perhaps, the problem is to determine the limits of variation in the number of cells in the pollen grains of Picea, and the relative frequency of the different numbers. Stated in that form, it is apparent that the abnormal, which is only the less frequent, is as much a part of the problem as the normal. The abnormal is only normal variation. Hence conclusions cannot be rejected because based on observation of abnormal structures.

After consideration of both the historical and original parts of this article it is obvious that variation in the number and arrangement of the cells found in the pollen grain and pollen tube is widespread among the families, genera, and species of gymnosperms. They occur in those species which usually have no disintegrating prothallial cells, as well as in those which have one or more such cells. These variations cannot be dismissed with the statement that they are abnormal, since the abnormal is only the less frequent modification. It seems to the writer that they may have a significance beyond the mere fact that the individual species vary.

A comparison between angiosperms and gymnosperms as regards the structure of the pollen grain recalls the well known difference. The essential structure of the pollen is much more uniform among the angiosperms, showing a spermatogenous cell usually free within the larger tube-forming cell, the whole structure to be regarded as probably a gametophyte reduced to an antheridium, the tube cell forming the antheridium wall, and generally there are no prothallial cells. Among the gymnosperms the structure of the pollen grain is not uniform in the different families and genera, and it is not so much reduced as in the angiosperms. In the more complex of the gymnosperms (Picea for example) there is not only an antheridium represented, but there may be from one to three disintegrating prothallial cells, and in addition the antheridium has a cell, the so called stalk cell, which has nothing to correspond to it in the angiosperms. This stalk cell is a sister cell to the so called body cell or central cell, which divides to form (usually) two sperm cells, and therefore corresponds to the spermatogenous cell in the angiosperms. In those gymnosperms with the simpler pollen grains no disintegrating prothallial cells are formed, but the stalk and central cells are uniformly present, the mother cell of these two being cut off at one side of the large tube-forming cell. In the pollen of the simplest gymnosperms therefore there is one cell more than in that of the angiosperms, that is the stalk cell. Cryptomeria seems nearer to the angiosperms in this particular than any other gymnosperm, since Lawson (:04) has found that the cell cut off at the side of the pollen grain is soon set free and lies within the cytoplasm of the large tube-forming cell. Chamberlain ('97) has also found cases in pollen grains of angiosperms which show one prothallial cell and more often it is found in angiosperm pollen that the spermatogenous cell is cut off at one side of the grain instead of lying free in the tube cell (Coulter and Chamberlain, :03, pp. 134–135).

The gymnosperms then, compose a group containing various transitional stages, as regards the pollen grain structure, between the very reduced condition characteristic of the angiosperms and the condition found among the pteridophytes in which the male gametophyte is more or less developed. Indeed some pteridophytes as Isoetes and Selaginella have more reduced male gametophytes than some gymnosperms, as Picea and Pinus.

The facts just presented suggest the question whether the gymnosperms at the present time are in a process of retrogressive modification in the direction of the condition found in the pollen of the angiosperms, or have the gymnosperms reached a condition of stable equilibrium, not so much reduced as that of the angiosperms and with different groups of genera stable at different stages in the reduction process.

The mental attitude of those investigators who insist on labeling a single prothallial cell as the second one implies a stable condition, with the number of cells formed invariable, and this mental attitude seems to be the common one among the writers on the subject. It seems to the present writer, however, that the number and wide distribution of the variations found among the gymnosperms may indicate that the gymnosperms, or at least some of them, are not in a state of stable equilibrium as regards the structure of the pollen grain, but that the process of reduction of the male gametophyte is in progress. In Picea, for example, a very few cases were found in which three vegetative prothallial cells were seen, 15.7 % of the grains counted showed two, 66.5 % showed one, and 3.8 % showed none. The number in others was uncertain. In the case of the double pollen grains divided into nearly equal parts, several showed no prothallial cell in one part, and a few showed none in either part. The extreme limits of variation in the number of prothallial cells in the pollen grain of *Picea excelsa* are therefore from 0 to 3, with 1 as the number of greatest frequency.

These facts do not *prove* that Picea is in a condition of progressive reduction of the male gametophyte, but at the very least they allow that interpretation, and it is set forth merely tentatively. Other investigations may either confirm or disprove it. Should further investigations confirm this conclusion we should have a case of a structure changed by gradual modification rather than by mutation. The occasional variations found in angiosperms in which the pollen grain shows a vegetative prothallial cell, or several tube nuclei, or the spermatogenous cell cut off at one side of the grain instead of lying free in the cytoplasm of the tube-cell (Coulter and Chamberlain, :03, p. 134–135) may possibly have a similar significance. If so, the condition now found in the pollen

of angiosperms also has come about by gradual modification, and the variations mentioned show that the "normal" structure is not so firmly fixed but that a small proportion of the grains produced reverts to a condition which was a stage in the gradual development. If this interpretation of the variations is rejected, then they must be looked upon as mutations, for whose cause we have nothing at all to suggest.

It is worth noting that among the gymnosperms the reduction of one structure in the pollen grain is not necessarily accompanied by the reduction of other structures in the same pollen grains. For example in Cupressus (Coker, :04) no sterile prothallial cell is cut off, and yet many sperm cells are formed instead of only two (Juel, :04). On the other hand, Picea, which may have as many as three sterile prothallial cells not only has the sperms reduced to two nuclei in one cell but even one of those nuclei has undergone a further reduction in size and only one, the larger, is functional (Miyake, :03). In the reduction of the sperm cells therefore, some of the gymnosperms have been modified to even a greater extent than the angiosperms. The degree of reduction seems to be closely associated with "use and disuse" of the parts concerned. Reduction of one of the sperm cells takes place only in cases where both could not function in fertilizing the egg. In the angiosperms the second sperm cell functions by uniting with the polar nuclei to form the endosperm, and this functioning whether a true fertilization or not, has been sufficient to prevent the reduction and possible suppression of one of the sperm cells.

The observations of Miyake (:03) that in *Abies balsamea* the second sperm nucleus may divide, or attempt to divide before it disintegrates in the upper part of the egg, and especially the observation that in one case this second sperm nucleus united with one of the second segmentation nuclei of the fertilized egg, is suggestive as to the possible way in which "double fertilization" may have arisen. The sperm nucleus that is left over after the union of the other one with the egg nucleus, has a tendency to unite with any nucleus that may be available, and in the angiosperms the polar nuclei offer the opportunity for such a union. It is not at all necessary that either of the polar nuclei be the homologue of an egg as Bonnier (:05) believes, in order to explain the union

with the male nucleus, since the latter has been shown to be able to unite with a purely vegetative nucleus, even of the sporophytic generation. This observation of Miyake's seems therefore to strengthen the evidence that the endosperm of angiosperms was vegetative phylogenetically (Coulter and Chamberlain, :03, p. 183), and to weaken correspondingly the view that it was strictly sexual in its origin (Bonnier, :05) and that the endosperm is to be regarded as a modified embryo.

If the introduction of the characters of the male parent into the endosperm modified that endosperm so as to make it produce food more suitable to the embryo with characters inherited from the same male parent (Sargent, :00, p. 708) then the embryo would be more vigorous, and more fit to survive in the struggle for existence than the one not nourished by such an endosperm Hence those individual plants in which "double fertilization" took place would finally become dominant in the competition with others of the same species.

The reduction, disintegration, and final complete suppression of the vegetative part of the male gametophyte may also depend on the law of "use and disuse." The vegetative cells of a well developed male gametophyte function chiefly in the process of photosynthesis. In most of the gymnosperms this function is impossible since the pollen grain is soon enclosed in the micropyle and light is excluded by the thick scales of the fertile cone. It is then a waste of energy and food materials to form cells that do not function, and this waste is only in part compensated for, if the cells formed disintegrate later and thus become available as food for the work necessary in forming sperms. Disuse leads to disintegration of the useless cells, and their complete suppression is the most advantageous condition of all.

It is interesting to note in this connection that in Araucaria which probably has the well developed male gametophyte, the pollen grain does not enter the micropyle (Thompson, :05), but germinates at the distal end of the ligule, more or less entangled on its serrated edge. From this point the pollen tubes pass in the grooves on the surface of the ligule or scale, a distance of an inch or more, to the micropyle. It would seem from this description of Thompson's that the pollen grains are exposed to the light during the development of the tubes, hence the multicellular male

gametophyte present may function in photosynthesis. Continued use has prevented in this case the reduction which took place in those species in which the pollen grain enters the micropyle directly.

In addition to the specific conclusions in regard to Picea (see pp. 270 and 275) the following more general ones are drawn, some of which are suggested rather than demonstrated:—

1. The variations in the male gametophyte and other structures in the pollen of gymnosperms, indicate that in this group there are examples of progressive reduction of some of those structures.

2. This reduction is by a gradual modification and not by mutation, and is due to the disuse of the vanishing structures.

3. The different structures are not necessarily reduced to a corresponding degree in the same species. ,

4. The suppression of the male gametophyte in gymnosperms is a distinct advantage where the function of photosynthesis is impossible to it.

5. The occasional prothallial cell in the pollen of angiosperms indicates that in this group also there was a reduction by gradual modification.

6. The division of the non-functional male nucleus in the egg of some of the gymnosperms and its fusion with a segmentation nucleus of the fertilized egg in *Abies balsamea*, strengthens the evidence for the view that the endosperm of angiosperms is phylogenetically a modified gametophyte and not a modified embryo.

7. The extremes in the variation of the male gametophyte among the genera of gymnosperms are found in Araucaria with a gametophyte of from 20 to 44 cells, (provided my interpretation of Lopriori's observation is correct) and *Cryptomeria japonica* (Lawson, :04), in which there is not only no vegetative male prothallium, but in which even the division wall between the tube nucleus and the primary spermatogenous nucleus is so fugitive as almost to escape detection.

The writer has no intention of making any further investigations along this line, as his special interests lie in another direction, but he felt that the opportunity to make the observations here recorded, though arising only incidentally, ought not to be neglected.

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ANATOMY OF *CRYPTOBRANCHUS ALLEGHENIENSIS*

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The Skeleton

The Skull

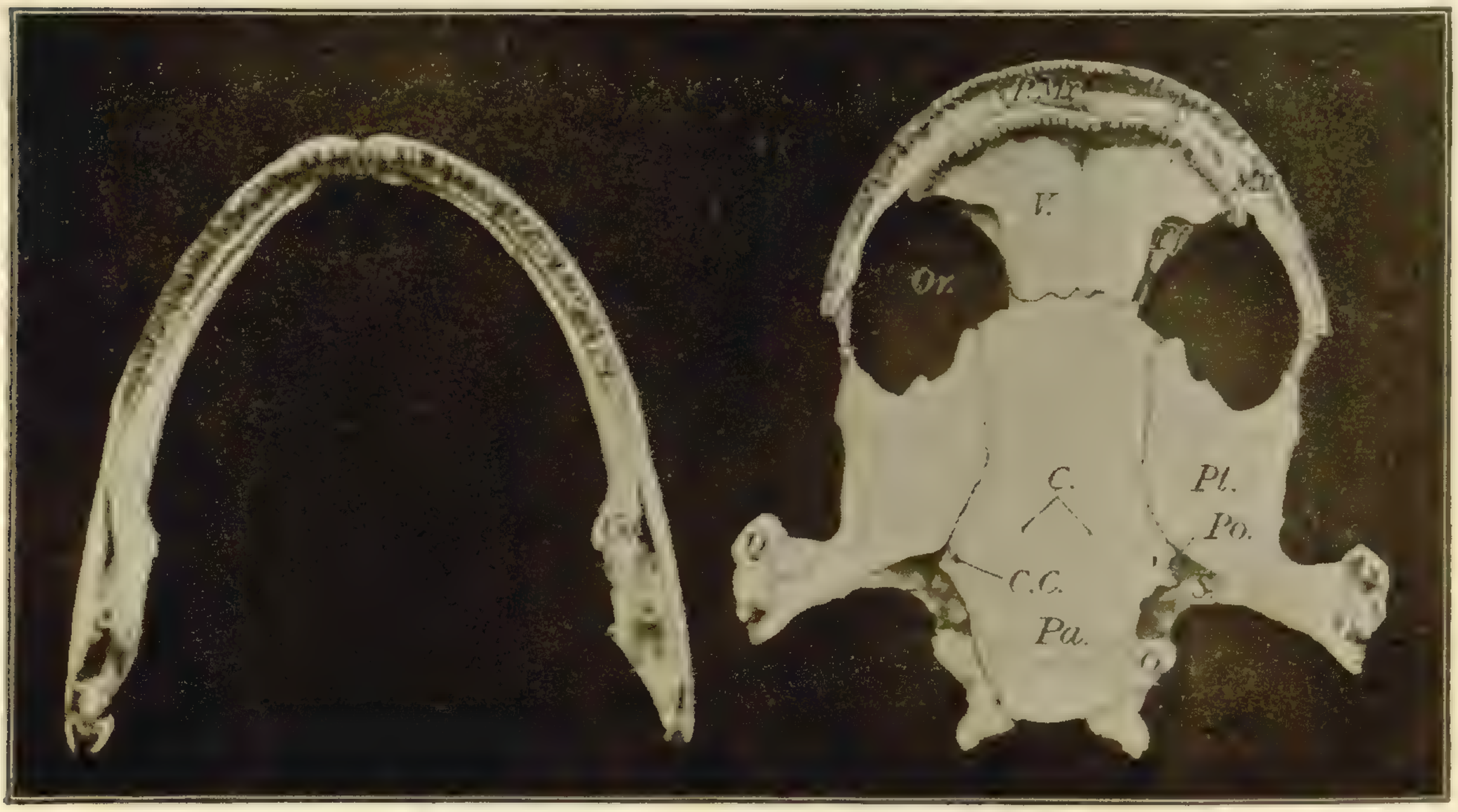
Since the skull of *Cryptobranchus allegheniensis* is strong and largely composed of bone, it is easy to prepare and to study. Figs. 1 and 2, A and B, are dorsal and ventral views of the skull proper and of the lower jaw, taken from photographs.

The skull as a whole has essentially the same structure as that of the Japanese giant salamander, described and figured by Osawa (:02), but it differs from the latter somewhat in general outline and in the shape of some of its constituent bones. Its length is greater in proportion to its width than is the case with the Japanese species, and the anterior outline of the head, formed by the maxillary and premaxillary bones, is more rounded in the American species, in which it forms an almost perfect arc of a circle. In the Japanese form the maxillæ and premaxillæ, as figured by Osawa, are relatively heavier than in the American species, and the posterior ends of the maxillary bones approach more closely the anterior borders of the pterygoids. The shape of the lower jaw is about the same in both species, but, if anything, is narrower in the American salamander, so that it does not fit with very great precision against the upper jaw. The anterior border of the skull is formed, as has been said, by the maxillary and premaxillary bones (Figs. 1, 2, 3, *Mx.*, *P. Mx.*), both of which are armed with numerous small, conical teeth, there being about 12 on each premaxilla, and 38 on each maxilla, making 100 teeth in the entire row.

The cartilaginous portions of the skull are not so extensive as in the Japanese salamander, and are superficially visible in the region of the anterior nares only, the anterior part of the orbit, the auditory region, and the articular surface of the quadrate.

A B

FIG. 1.—A. Ventral view of the mandible. B. Dorsal view of the skull (from a photograph). *A.*, angular; *Co.*, coronoid; *Ct.*, opening of canal ("canalis cordæ tympani"); *D.*, dentary; *E.*, ethmoid; *E. C.*, ethmoidal canal; *F.*, frontal; *Mx.*, maxillary; *N.*, anterior nares; *Na.*, nasal; *O.*, exoccipital; *O. F.*, occipital foramen; *Or.*, orbit; *P.*, parietal; *Pf.*, prefrontal; *P. Mx.*, premaxillary; *Pt.*, pterygoid; *Q.*, quadrate; *S.*, squamosal.



A B

FIG. 2.—A. Dorsal view of mandible. B. Ventral view of skull (from a photograph). *A.*, angular; *C.*, minute canals through parasphenoid; *C. C.*, carotid canal; *Co.*, coronoid; *D.*, dentary; *Mx.*, maxillary; *O.*, exoccipital; *Or.*, orbit; *Pa.*, parasphenoid; *P. Mx.*, premaxillary; *Po.*, proötic; *Pt.*, pterygoid; *Q.*, quadrate; *S.*, squamosal; *V.*, vomer.

The bony cranium will first be described, and then a brief description of the cartilaginous cranium will be given.

The *premaxillæ*, forming the extreme anterior tip of the skull, are firmly united with each other in the middle line, and articulate less closely, on each side, with the adjacent maxillæ. Their dorsal surface is prolonged backward somewhat, to articulate with the anterior borders of the nasals. Between them, in the mid-dorsal line, is a small foramen, and each of them exhibits a small foramen on its anterior surface (Fig. 1, *P. Mx.*). Their antero-ventral border is armed with the teeth above mentioned, while the postero-ventral border articulates with the anterior border of the vomers (Fig. 2, *P. Mx.*, *V.*). About half of the median border of the nasal opening (*N.*) is formed by the premaxilla.

The two *maxillary* bones (*Mx.*) form the rest of the upper jaws, and make up, in fact, about three fourths of their extent. Their entire ventral border is armed, as has been described, with a single row of teeth. The medial end of their arc is in articulation with the premaxillary, while the lateral end tapers somewhat and is connected with the anterior angle of the pterygoid by a tough band of connective tissue. On the dorsal aspect of the maxillary, near the medial end, a triangular projection extends in a postero-medial direction between the frontal and the prefrontal. On the anterior border of each maxilla, at the base of the triangular projection just described, are two small openings, the infra-orbital foramina.

The *nasals* (Figs. 1 and 3, *Na.*) lie just back of the premaxillæ and form the posterior half of the median border of the anterior nares (*N.*). The two bones, when taken together, have somewhat the shape of an arrowhead, the tip of the head pointing towards the base of the skull. The base of the arrowhead articulates anteriorly with the posterior projections of the premaxillæ that have already been mentioned. In the mid-dorsal line the two nasals articulate closely with each other, while their postero-lateral borders articulate with the frontal bones. The anterior half of each nasal is closely united, ventrally, with the dorsal side of the corresponding vomer, and thus helps to form the septum between the two nasal chambers.

The *frontals* (*F.*) are two large, much elongated bones that lie

just posterior to the nasals and form a considerable part of the roof of the skull. Like the nasals, these two bones, when taken together, have somewhat the shape of an arrowhead, the tip of the head again being towards the posterior. Along the middle line, where the bones articulate with each other, is sometimes seen a well marked ridge. Each frontal forms the posterior half of the lateral border of the corresponding nasal opening, and articulates laterally with the maxillary, prefrontal, and parietal; anteriorly with the nasal, and medially with its fellow of the opposite side. Ventrally the frontals are more or less closely united with part of the cartilaginous cranium, to be described later.

The *prefrontals* (*Pf.*) are two elongated bones in the roof of the skull, on the antero-medial border of the orbits. Each bone articulates anteriorly with the corresponding maxilla, medially with the frontal, and posteriorly with the extreme anterior end of the parietal.

The *parietals* (*P.*) are two large bones that form the greater part of the roof of the cranial cavity. The posterior half of each bone is broad and angular, while the anterior half is long and narrow, and extends forward to articulate with the posterior end of the prefrontal, as has already been stated. The posterior halves of the two parietals articulate with each other, but the narrow anterior portions are separated from each other, and into the space thus formed the posterior ends of the two frontals project and articulate. The narrow, anterior part of the parietal overlies and is more or less closely attached to the ethmoid, presently to be described. The broad, posterior part of the parietal articulates laterally with the squamosal, and posteriorly with the lateral occipital. The sagittal suture, between the two parietal bones, extends back to the antero-dorsal border of the foramen magnum. A very small portion of this border is formed by the medio-posterior extremities of the parietals.

The *ethmoids* (*E.*) will be described at this place, although they are partially composed of cartilage even in the adult, and are described by Osawa in connection with the cartilaginous cranium. The ossified portion of the ethmoid is shown at *E.* in Figs. 1 and 3. It is an elongated rod of bone, attached dorsally to the parietal, as has been mentioned, and ventrally to the parasphenoid

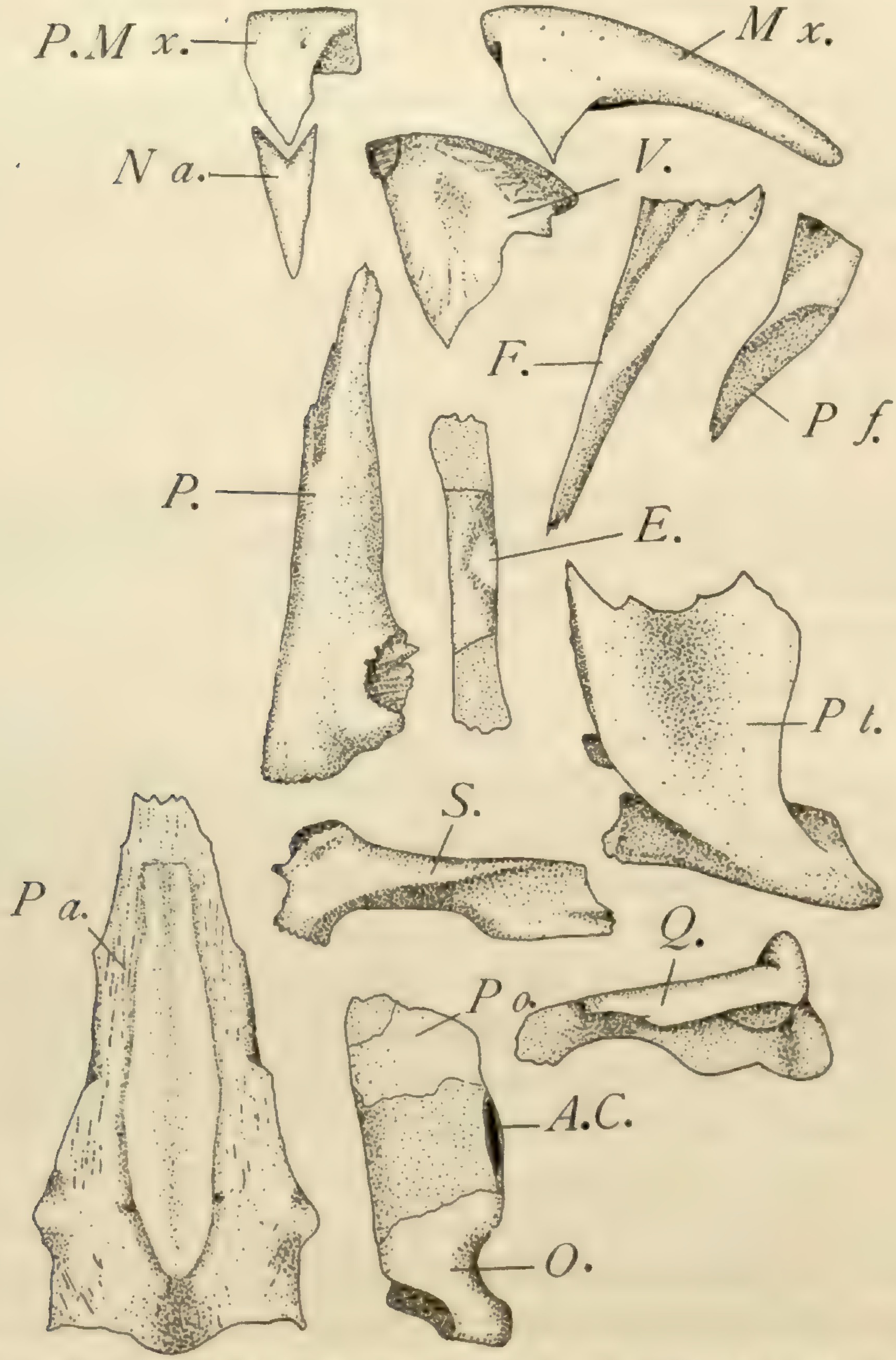


FIG. 3.—The bones of the skull, disarticulated. *A. C.*, opening of the auditory capsule; *E.*, ethmoid (cartilaginous at each end); *F.*, frontal; *Mx.*, maxillary; *Na.*, nasal; *O.*, exoccipital; *P.*, parietal; *Pa.*, parasphenoid; *Pf.*, prefrontal; *P. Mx.*, premaxillary; *Po.*, proötic; *Pt.*, pterygoid; *Q.*, quadrate; *S.*, squamosal; *V.*, vomer.

and, slightly, to the pterygoid. Extending laterally through the midventral region of this osseous part of the ethmoid is a small ethmoidal canal (*E. C.*). Anteriorly and posteriorly the osseous ethmoid is continuous with the cartilaginous cranium of the nasal and the occipital regions.

The *pterygoid* (*Pt.*) has, with the exception of the parasphenoid,

a greater surface than any bone in the skull. Seen from the dorsal aspect, it is nearly rectangular in outline, but seen from the ventral side, it exhibits a long, postero-laterally projecting process which underlies the squamosal and quadrate bones. Its anterior and lateral borders are thin, and the former makes the irregular outline of the posterior border of the orbit. The antero-lateral corner is connected with the maxillary by a band of connective tissue, as has already been pointed out. The median border underlies the ethmoid to a slight extent, and is attached ventrally to the side of the parasphenoid. The posterior border is hidden, in a dorsal view, by the squamosal and quadrate, with which it articulates. The above-mentioned postero-laterally projecting process of the pterygoid is an elongation of the lateral and posterior borders, and extends entirely across the squamosal until it shows behind it, and forms a part of the articular surface for the lower jaw. This projection of the pterygoid behind the squamosal and quadrate is shown in Fig. 1. The pterygoid is somewhat arched from side to side, with the convexity of the arch dorsad. Above the postero-median corner of the pterygoid, in the angle between the ethmoid, the parietal, and the squamous, is a marked depression (see Fig. 1) covered in life by a membrane. In the bottom of this depression several canals leading into the cranial cavity may be seen. One of these canals is much larger than the others, and is said by Osawa to be for the exit of the trigeminal nerve. At the postero-lateral corner of the depression is a short canal, formed by a narrow space left between the squamosal above and the pterygoid below. This canal does not lead into the cavity of the skull, but extends backward to the outer side of the auditory capsule, and seems to be an anterior continuation of the vertebral canal; it is apparently the canal that Osawa calls the palatine.

The *squamous* bones (*S.*) are among the most important in determining the shape of the skull. They are elongated, rod-shaped bones that extend laterally, at right angles to the long axis of the skull, and form the square outline of its base. Each bone has the appearance of being slightly twisted, due to a well marked dorsal ridge that extends nearly its entire length. The medial end of the bone is somewhat flattened and enlarged, and articulates with the side of the parietal near its posterior end.

The distal end of the squamosal is firmly united with the enlarged end of the quadrate, and partially overlies that bone. Ventrally the squamous articulates with the posterior border of the pterygoid as has been described.

The *quadrate bones* (*Q.*) are two small bones that form almost the entire articular surfaces for the lower jaw. A small portion of these surfaces, however, is formed by the pterygoids. Each quadrate is a small, triangular bone lying at the distal end of the squamous above described, and largely covered by it. The heavy, basal portion of the bone projects beyond the end of the squamous and, together with the tip of the pterygoid, is covered with a thick pad of cartilage for articulation with the lower jaw. The slender, medially projecting portion of the bone lies anterior and ventral to the squamous, and dorsal to the pterygoid. It is more closely attached to the former than to the latter bone. Osawa figures the quadrate in the adult skull as entirely of cartilage, and describes it with the cartilaginous cranium, but in the present form it is quite fully ossified.

The *tympanic bones*, described by Osawa in the Japanese species, could not be determined.

The *exoccipitals* (*O.*) form the greater part of the border of the occipital foramen. Each bone presents a postero-laterally projecting condyle, for articulation with the first vertebra. Through the base of this condyle passes a horizontal canal of considerable size into the posterior part of the cranial cavity. This canal is probably for the exit of the vagus nerve. The anterior part of the exoccipital is much enlarged and is hollowed out to form the posterior half of the auditory capsule. The dorso-anterior borders of the exoccipital articulate with the posterior end of the parietal, while the ventral border articulates with the posterior end of the parasphenoid.

The *occipital foramen* or foramen magnum is markedly triangular in outline, especially when seen from the dorsal aspect. The apex of the triangle, which lies at the posterior end of the sagittal suture, is some distance in front of the base, so that the plane of the aperture, instead of being vertical, slants in a dorso-anterior direction. Only a small portion of the base or ventral border of the foramen is formed by the parasphenoid.

All of the bones described above are seen in a dorsal view of the skull; those of the bony cranium that will now be described, are best seen from the ventral aspect.

The *parasphenoid* (*Pa.*) is the only unpaired bone in the skull, and is larger than any other single bone. It forms practically the entire floor of the cranial cavity, as seen from the exterior. The bone as a whole has somewhat the shape of a broad, blunt-pointed dagger, with the point towards the anterior end of the skull, and partially concealed, in a ventral view, by the posterior ends of the vomers, with which it articulates (*Pa.* in Figs. 2 and 3). Laterally the parasphenoid articulates, for the anterior half of its length, with the pterygoids. Just posterior to the pterygoids it articulates dorsally with the small proötics, and posterior to the auditory foramen it articulates with the exoccipitals. Its extreme posterior end forms the ventral border of the occipital foramen. A short distance anterior to this point is seen, in some specimens, a well defined, irregular transverse line (Fig. 2), which would seem to indicate the presence of a basioccipital bone, but as no separation of the bone along this line could be effected, the presence of a definite basioccipital could not be determined. On each side of the parasphenoid, close to its point of union with the proötic, is a canal (*C. C.*), leading into the cranial cavity, called by Osawa the carotid canal. Nearer the midventral line, somewhat anterior to the preceding, are two very small openings (*C.*), probably for the entrance of minute blood vessels. The ventral surface of the parasphenoid is smooth and nearly flat, except at the anterior end where it is more or less convex, with a slight median ridge that fits in between the posterior ends of the vomers.

The *vomers* (*V.*) are the large flat bones that form the base of the anterior end of the skull and the floor of the nasal cavity. They may, perhaps, be considered as formed of the fused vomers and palatines. Each bone is roughly triangular in outline, one side of the triangle being fused with the corresponding side of the other bone in the midventral line. Another side, which is rather deeply indented by a sort of bay, forms part of the inner border of the orbital space; and the third side, which is in the form of an arc and is armed with teeth, is attached to the maxilla and premaxilla. The row of teeth, lying on anterior borders of the two vomers,

forms an arc that is almost exactly concentric with the arc of the premaxillæ and maxillæ, except that there is a slight depression in the middle where the two vomers meet. The anterior half of the median edge of each vomer is elevated dorsally into a ridge, and the median elevation formed by the union of these ridges separates the nasal chamber into its two parts, and unites the vomers below with the nasals and the premaxillæ above. It forms, in other words, the bony nasal septum.

The *proötics* (*Po.*) are two small bones of irregular shape that form the antero-dorsal borders of the auditory capsules. Even in the adult they are largely composed of cartilage, so that in the dried skull they scarcely show from either the dorsal or the ventral side. They are more closely united to the parasphenoid than to any other bone, but they also articulate with the cartilaginous posterior end of the ethmoid, with the parietals, with the squamous bones, and, possibly to a slight extent with the pterygoids. There are several canals that lead from the exterior to the cranial cavity, in the neighborhood of the proötic. Of these the largest has already been mentioned in connection with the pterygoid bone, and is said by Osawa to be the trigeminal foramen. It is a break in the median border of the proötic, rather than an actual canal through the bone. The only other canal in this bone that can be made out without difficulty is the facial, which lies in the edge of the bony part of the proötic, just dorsal to the carotid canal, and runs transversely through the bone to the cranial cavity.

Columella auris is the name given to two very small bones that are found in connection with the auditory capsules. Each columella is fan-shaped or palmate in outline, and, on account of its minute size and loose attachment to the rest of the skull, is easily lost in the preparation of the skull. The broad part of the bone is connected by cartilage with the foramen ovale of the auditory capsule, while the narrow end (the handle of the fan) projects laterally and, according to Osawa, is connected by cartilage with the quadrate, though this latter point could not be determined in the present species. The columella does not show in either of the figures of the skull.

The cartilaginous cranium will now be described. It may be divided, to use the terms adopted by Osawa, into two general

regions, an anterior naso-ethmoidal and a posterior petroso-occipital, regions which are connected by two narrow longitudinal bands in the position of the ethmoids. The space between these bands is the pituitary space, and the bands themselves are ossified in their middle regions to form what we have already described as the ethmoid bones, while their ends are cartilaginous to connect anteriorly and posteriorly with the naso-ethmoid and petroso-occipital regions respectively.

The *naso-ethmoid cartilage* serves chiefly as a lining to the nasal chamber, and may be seen in a dorsal view of the skull, over a part of the anterior nares and at the antero-lateral angle of the orbital space.

The *petroso-occipital* region is more extensive, and the cartilage is there thicker than in the naso-ethmoidal region. It forms, as the name would suggest, the cartilaginous basis of the occipital region, and though in the adult it is largely ossified, there is a considerable cartilage that persists even in the adult skull. The thickest cartilage is found in the region of the ear, where it forms a large part of the auditory capsule. Various parts of the petroso-occipital region are more or less fully ossified to form the following bones, whose form and position have already been described, and which are described by Osawa in connection with the cartilaginous cranium: the exoccipital (occipitale laterale), the proötic, the quadrate, and the columella. The ethmoid, which forms the middle of the longitudinal bands connecting the petroso-occipital and naso-ethmoidal regions, has also been described in connection with the bony cranium.

It remains now to describe the bones and the cartilages of the visceral skeleton.

The Visceral Skeleton

The *visceral skeleton* is made up of six arches: the mandibular arch or lower jaw, the hyoid arch, and four visceral arches. It differs, then, markedly from the Japanese species which, according to Osawa, has only four arches, the last two visceral arches being absent. The visceral skeleton as a whole is large and strong and, though consisting largely of cartilage, it persists throughout

life. It forms the supporting framework to the floor of the capacious mouth and throat so important in the process of inspiration.

The *mandible* or lower jaw (Figs. 1, 2, 4) is made up of two distinct parts, joined together anteriorly, in the middle line, by a short ligament of cartilage, the mandibular symphysis. As may be seen from the figures, the curve of the anterior margin of the mandible is not so wide as that of the upper jaw, so that the two jaws do not fit together very closely. Each half of the mandible is made up of three elements: the dentary, the coronoid, and the angular.

The *dentary* (*D.*) is the largest of these three bones, and extends from the symphysis almost to the posterior angle of the jaw. Its anterior end is thick and rounded, while the posterior end is thin and pointed to fit against the outer surface of the angular. The ventro-anterior surface of the dentary is smooth, and is marked by a series of about six small openings, mental foramina, which do not show in either a ventral or a dorsal view of the mandible. The dorso-posterior, or upper-and-inner, border of the dentary is depressed to form a deep alveolar surface, along the outer border of which are situated the small, conical teeth in a single row. There are about forty-five teeth in each dentary. The alveolar surface extends for somewhat more than two thirds of the entire length of the bone, and ends posteriorly at the point where the dentary meets the outer border of the coronoid. The teeth are all of nearly the same size, except that those at the posterior end of the row are slightly smaller than the rest. They are attached to the bottom and side of the alveolar depression, so that their crowns sometimes project but a short distance above the upper border of the dentary bone.

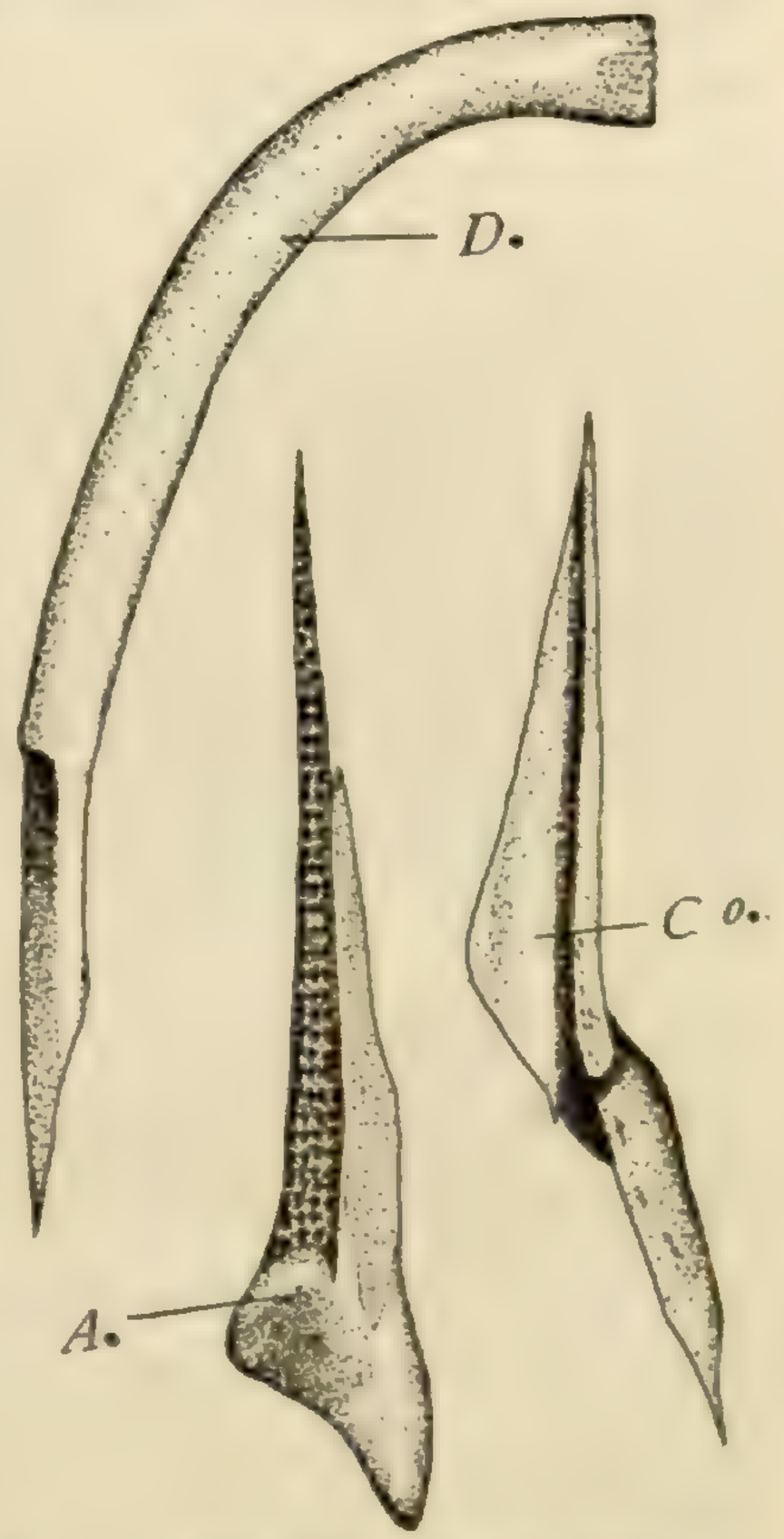


FIG. 4.—The bones of the mandible, disarticulated. *A.*, angular; *Co.*, coronoid; *D.*, dentary.

Individual teeth are frequently broken off, but whether they are ever regenerated again the writer is not able to say.

The *coronoid* (*Co.*) is a spindle-shaped bone that lies on the inner side of the mandible near its posterior end. Its inner or medial surface is smooth and rounded except near the middle of its length, where it is elevated and roughened to form the coronoid process for the attachment of muscles. In the anterior corner of the triangular depression between the dorsal borders of the dentary and coronoid bones is a small canal leading towards the anterior end of the jaw. It may be called the alveolar canal. A ventral view of the jaw shows a more evident canal (*Ct.*) entering between the dentary and coronoid bones, just at the anterior end of the angular, as seen from the surface but really at some distance behind this end as the anterior portion of the angular is hidden between the two other bones. This canal corresponds, perhaps, to the inferior dental foramen of higher forms. The canal that Osawa describes, in this region, passes directly through the coronoid bone; he calls it the "canalis chordæ tympani." The outer surface of the coronoid (hidden, of course, by the other bones) is deeply grooved longitudinally to receive a long, slender process of the angular (Fig. 4).

The *angular* (*A.*) forms the posterior end of the mandible and presents there an articular surface for attachment to the quadrate. This articular surface is triangular in outline, with the apex of the triangle towards the posterior. The articular portion of the angular is a thick mass of cartilage, and extends forward to fill the angular space between the dentary and coronoid bones that has already been mentioned. Anterior to this angular space, this cartilage is continued forward as a long, slender rod (Meckel's cartilage) lying in a furrow between the dentary and the coronoid. Meckel's cartilage extends for nearly three fourths of the length of the jaw, or to about the middle of the row of teeth. The part of the angular that is seen from the ventral aspect (Fig. 1, A) is ossified, and extends, as may be seen from the figure, for some distance, anteriorly, between the dentary and the coronoid. In fact it extends farther in an anterior direction than is seen from the surface, being covered for some distance by the coronoid.

The *hyoid apparatus* (Fig. 5), using that term to include both

the hyoid and the visceral arches, has, as may be seen from the figure, a very complicated structure. It differs from the same apparatus in the Japanese salamander in having two more visceral arches, as has been said; also in the relative amounts of bone and cartilage, and in the general form of the constituent parts. The arches will now be described in order, from before backward.

The *hyoid arch* (*H.*, *H'.*, *C.*) is, as would be expected, much the largest of the arches, and is composed of two S-shaped bars united medially by a small, unpaired copula (*C.*). Each bar is made up of two closely united segments (*H.*, *H'.*), of which the anterior one (*H'.*) is nearly straight and is united with the copula, while the posterior one (*H.*) is strongly curved outwards at its free or posterior end where it ends in a cartilaginous surface for articulation with the skull. As may be seen in the figure, nearly half of the posterior segment of the hyoid arch is bony (the cartilaginous portions being, in all cases, dotted). In the Japanese form the entire hyoid arch is composed of cartilage, and each bar is of a single piece, instead of being of two pieces as in the present form. The copula or median connecting piece is of about the same shape in both species, and consists of a short transverse portion with a pointed knob projecting in a postero-dorsal direction. The elements of the hyoid arch are flattened in a dorso-ventral direction, so that they are elliptical in cross section. The whole hyoid arch has somewhat the shape of a wide letter U, with the free ends of the letter bent widely apart. Into the space between the two bars of the hyoid arch projects the

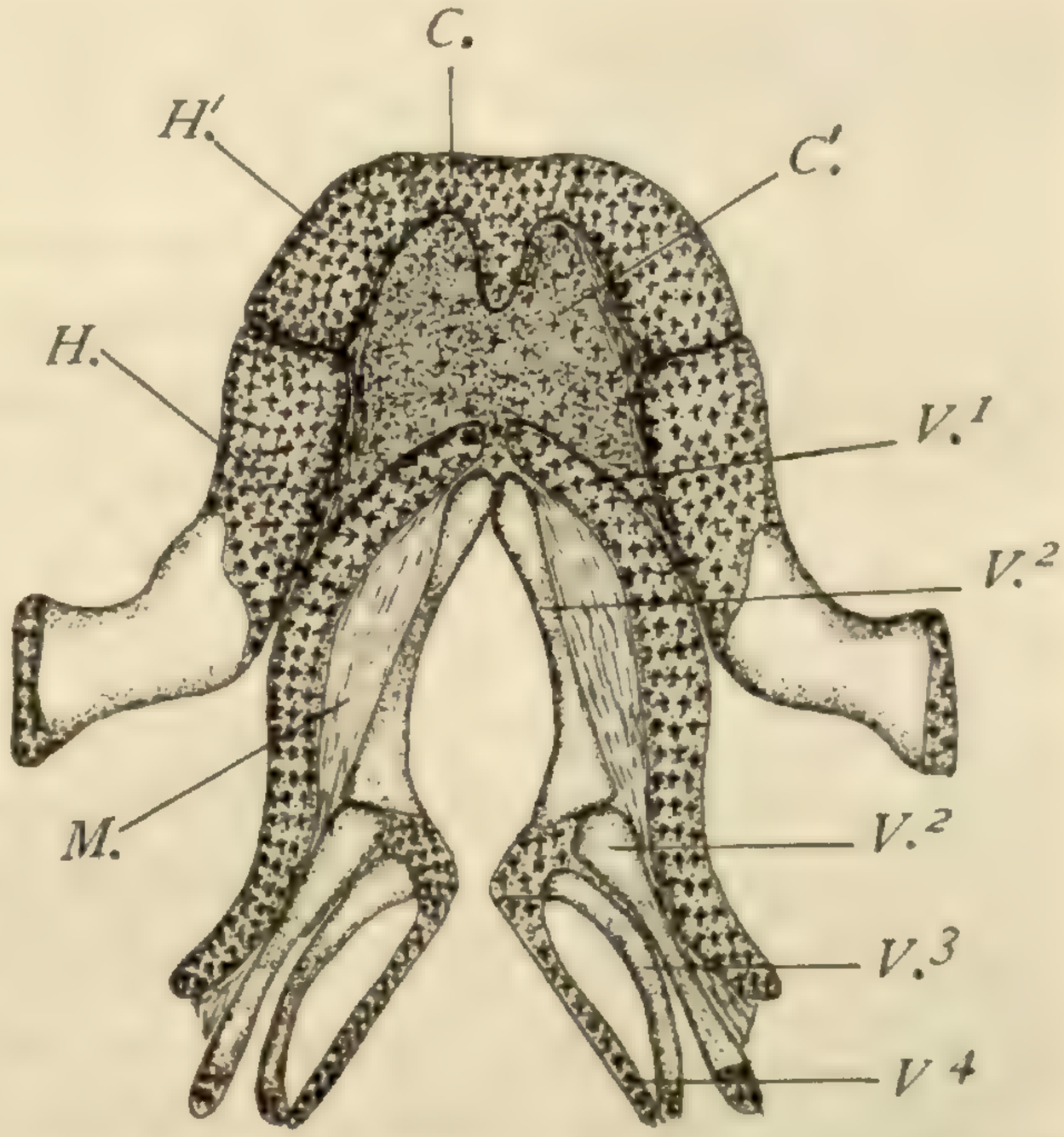


FIG. 5.—The hyoid apparatus. *C.*, copula of hyoid arch; *C'.*, copula of first and second visceral arches; *H.*, *H'.*, elements of the hyoid arch; *M.*, membrane between the first and second visceral arches; V^{1-4}., first to fourth visceral arches.

flat, cartilaginous copula (*C'*.) of the first and second visceral arches. It is flat, broadly heart-shaped in outline, and is composed of soft, fibro-cartilage. It is united around its periphery with the inner border of the hyoid arch by a thin but tough connective-tissue membrane. On the midventral line of this copula, at its posterior edge, in a slight cartilaginous elevation to which are attached the anterior ends of the first and second visceral arches, the former to its lateral, the latter to its posterior border.

The *first visceral arch* (*V* ^{1}.) is composed of two slender, somewhat flattened, S-shaped bars united in the median line by the copula that has already been described. Each bar of this arch is composed of a single rod of firm, translucent cartilage. Along its entire median border this arch is united, by a tough, fibrous membrane, to the outer border of the *second visceral arch* (*V*^{2}.) which, in distinction to the preceding arches, is composed almost entirely of bone. Its constituent bars, instead of being S-shaped, are practically straight laterally though somewhat arched in a dorso-ventral direction. Viewed from the ventral aspect, the two bars of this arch form an almost perfect letter V. Each bar is formed of two elongated bones, of which the anterior or dorsal one is the longer. Both bones are nearly circular in cross section, and are enlarged at each end, the two adjacent ends being the larger, and somewhat flattened. The free end of the posterior or ventral bone is tipped by a small piece of cartilage.

Between the two bones of the second visceral arch, on each side, is a small pad of cartilage which extends medially and becomes spread out for the attachment of the anterior ends of the *third* (*V*^{3}.) and *fourth* (*V*^{4}.) *visceral arches*, of which the former is composed almost entirely of bone, and the latter entirely of cartilage. The third and fourth arches are formed of distinct bars; that is, they are not united in the midventral line by a copula as are the preceding arches. The bars of the third and fourth arches on each side are united with each other at both ends, and form a loop which serves to stiffen the border of the permanent gill slit. The third bar is of bone, and is tipped at the posterior end with a small head of cartilage for attachment to the corresponding end of the fourth bar. This bar is cylindrical in cross section, and is slightly curved, so that the loop is kept permanently open, while

the elasticity of the cartilaginous fourth bar allows considerable variation in the size of the loop and consequently in the size of the gill slit. The anterior end of the third bar is united, for a short distance, with the posterior bone of the second bar by the same tough membrane that was noted in connection with the more anterior arches.

The Vertebral Column

The vertebral column of the American salamander (Fig. 6) consists of from 39 to 42 bones or vertebræ. The giant salamander of Japan, according to Osawa, has in its vertebral column forty-five vertebræ, besides two cartilaginous rudiments at the tip of the tail. The vertebræ may be divided into three sets: those of the body, of which there are 19; those of the tail, 19 to 22 in number; and a single vertebra between these two sets, the sacrum. The number of body vertebræ, as might perhaps be expected, seems to be more constant than the number of caudals, though the variation in the latter may be partly due to the great difficulty of preserving the last few vertebræ on account of their small size and cartilaginous nature. All of the vertebral centra, with the exception, of course, of the anterior surface of the first, are deeply amphicœlous. The anterior and posterior concavities are so deep that they almost meet in the middle of the centra. There is, however, no continuous passage through the centra.

FIG. 6.—Dorsal view of the entire vertebral column, with the ribs attached (from a photograph).

As a type of the body vertebræ, or those lying anterior to the sacrum, the tenth vertebra may be described (Figs. 6 and 7). As is seen in Fig. 7, D, a lateral view, the centrum is distinctly hourglass-shaped, and its length is about twice its greatest diameter. Like all of the other body vertebræ, except the first, this vertebra

has strongly developed transverse processes (Figs. 6, 7, 8, *T.*), to which are attached short, thick ribs (*R.*). These ribs, like the processes to which they are attached, are flattened in an antero-posterior direction, so that, at their points of attachment, they are considerably thicker in a dorso-ventral direction than they are in an antero-posterior direction. The ribs, with the exception of those attached to the sacrum (to be presently described), stand out at right angles from the vertebræ, and taper to a sharp, round point. In the anterior part of the body the ribs are somewhat longer than the processes to which they are attached, while in the region near the sacrum they are shorter. The transverse processes are of about the same length on all of the body vertebræ, and project rather strongly towards the posterior. The base of

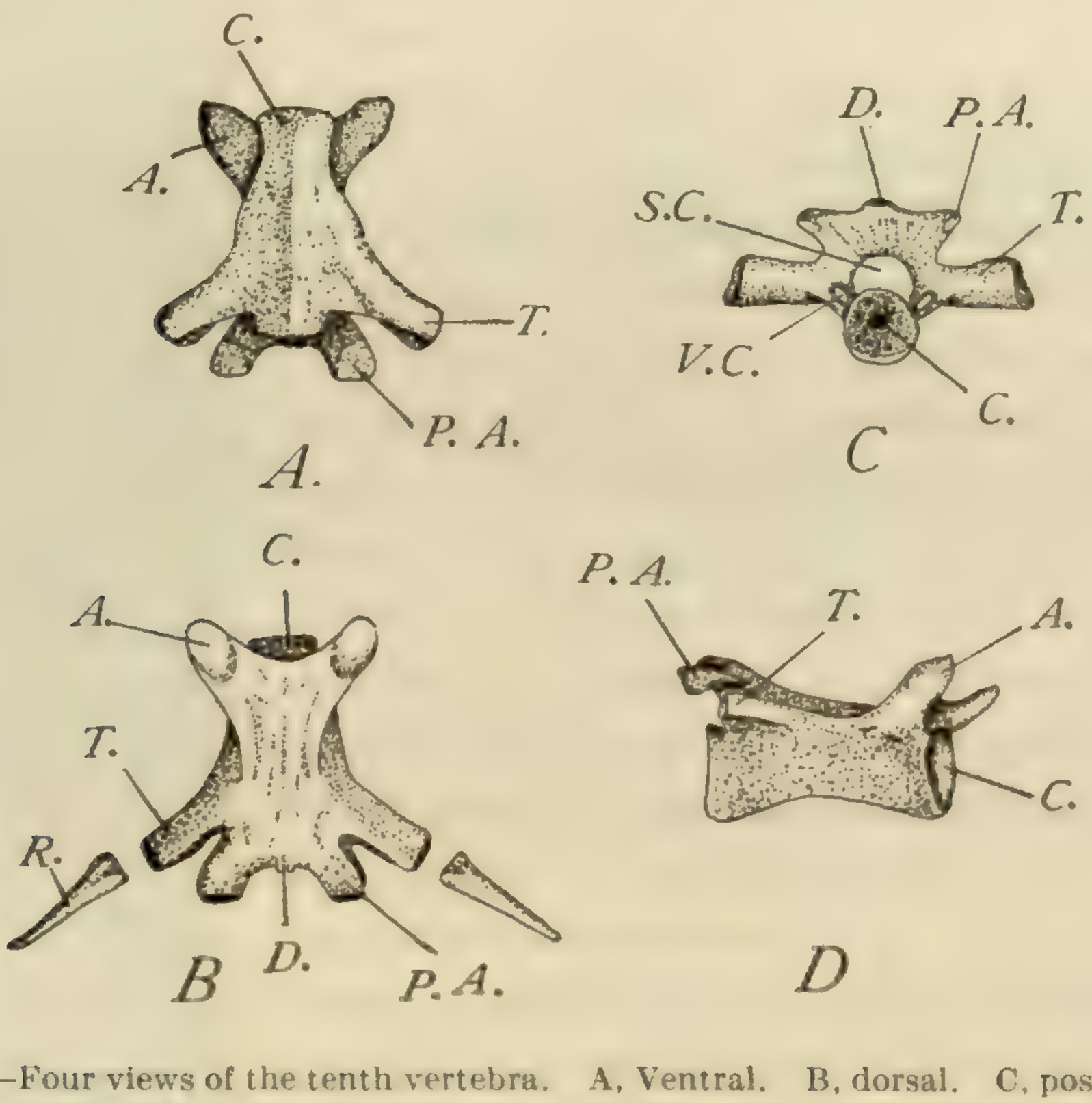


FIG. 7.—Four views of the tenth vertebra. A, Ventral. B, dorsal. C, posterior. D, lateral. *A.*, anterior articular process; *C.*, centrum; *D.*, dorsal spine; *P. A.*, posterior articular process; *R.*, rib; *S. C.*, spinal canal; *T.*, transverse process; *V. C.*, vertebral canal.

each transverse process is perforated by a small vertebral canal (Fig. 7, *V. C.*). The dorsal or spinous process (Figs. 7 and 8, *D.*) is small and inconspicuous in all of the body vertebræ, and is most prominent on the first.

The posterior articular processes (Fig. 7, *P. A.*) have a rounded outline, as seen from above, and are flattened ventrally where they articulate with the underlying anterior processes of the succeeding vertebra. The anterior articular processes (Fig. 7, *A.*) do not differ greatly from the posterior, except in having their articular surfaces on the dorsal instead of the ventral side. The vertebræ of the body region resemble each other so strongly in shape that it would be very difficult to say from just what part of the body any given vertebra had been taken, but in an individual skeleton the vertebræ in the middle region of the body are both longer and heavier than those anterior and posterior to them.

The sacral vertebra differs from those immediately in front and behind it only in the much greater development of the transverse processes (Fig. 6, *S.*), and the ribs. The sacral ribs, since they serve for the attachment of the pelvic girdle, are much heavier and stronger than any of the other ribs. Instead of projecting as sharp points straight out from the body, they curve downward and end in articular surfaces for the attachment of the upper ends of the two rods of the ilium.

The caudal vertebræ present more variations both in size and form than do those of the body. The first caudal vertebra so closely resembles the last body vertebra that it would be very difficult, if not impossible, to tell them apart. The third caudal vertebra may be described as a type of those of this region (Figs. 6 and 8). The chief differences between this vertebra and the typical body vertebra are, besides the smaller size of the former, the weaker transverse processes, the larger dorsal spine, and the presence of a well developed hæmal arch. Transverse processes are found on the first eight of these vertebræ, and are provided, at least in the case of the first four or five, with minute ribs. These processes diminish in size from before backward, so that those of the eighth caudal vertebra are very small (Fig. 6). The dorsal spines, on the other hand, become more prominent from before backward, until they reach their greatest development in the midcaudal region, or, at any rate their greatest relative development. As the caudal vertebræ become more and more compressed laterally, the posterior articular processes approach each other until, in the midcaudal region, they are not distinguishable from the

large dorsal process. Even in the third caudal, these processes (Figs. 6 and 8, *D.*, *P. A.*) have the appearance of being mere articular surfaces on the sides of the spinous process. The anterior articular processes (Figs. 6 and 8, *A.*) also diminish in size towards the posterior until, on the last few vertebræ, they, like the posterior articular processes, practically disappear, and the vertebræ in this region are united by their centra only.

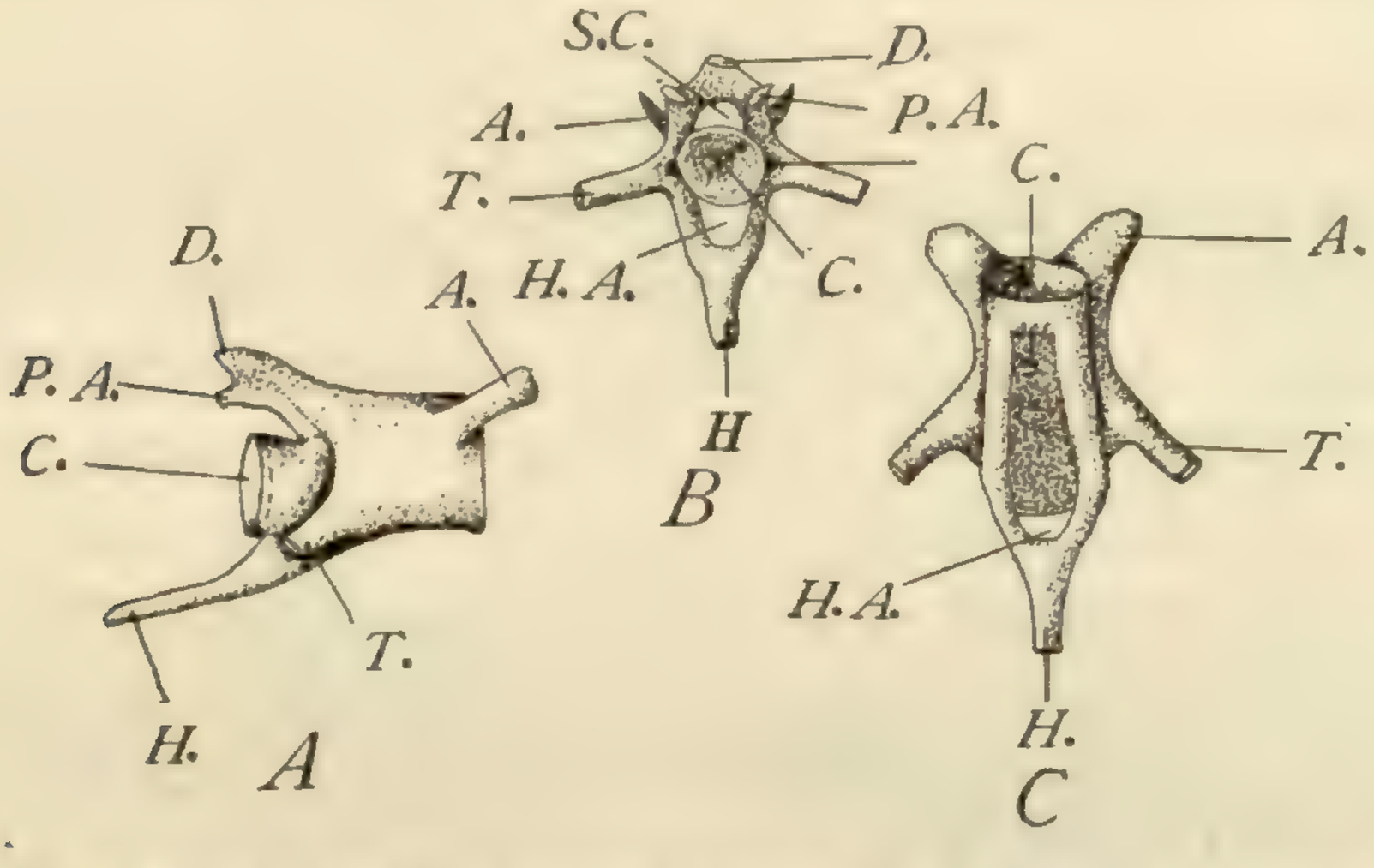


FIG. 8.—Three views of the third caudal vertebra. A, lateral. B, posterior. C, ventral. *A.*, anterior articular process; *C.*, centrum; *D.*, dorsal spine; *H.*, hæmal spine; *H. A.*, hæmal arch; *P. A.*, posterior articular process; *S. C.*, spinal canal; *T.*, transverse process.

The hæmal arch, which is characteristic of the caudal vertebræ, is well developed on the third vertebra (Fig. 8, *H. A.*), in which the two sides of the arch are prolonged ventrally into a long spine (*H.*). As may be seen in Fig. 8 the canal formed by the hæmal arch is larger than the spinal canal; this is true of all the caudals except the first, which is without a hæmal arch.

The hinder caudal vertebræ, besides being laterally compressed, show an actual concavity in each side of their centra.

The two cartilaginous rudiments at the end of the tail, that are described by Osawa, I have not been able to determine, though I am not willing to say that they do not exist in the American as well as in the Japanese form. There is, however, except in the number of vertebræ, a strong resemblance between the vertebral columns of the two animals.

Skeleton of the Appendages

The Anterior Extremity.— Both pairs of appendages are small and weak, and the two girdles are largely made of cartilage. The shoulder girdle is almost entirely composed of cartilage, and the scapular, which is small, is the only part that is bony.

The *sternum* (Fig. 9) is so small and is composed of such thin cartilage that it may easily be overlooked in a hasty dissection. It lies in the usual midventral position, and is overlapped anteriorly for about half of its length by the large coracoids, that is to say, the coracoids overlap it on its ventral side. In a medium-sized specimen it is about 2.5 centimeters long and of nearly the same width. It is somewhat shovel-shaped, with the rounded edge towards the anterior (Fig. 9). The ventral aspect is smooth and slightly convex, while the dorsal side is correspondingly concave, and is provided with a V-shaped thickening, which projects slightly in an antero-dorsal direction. It is chiefly by this thickening that the sternum is attached to the body wall. The edges of the sternum thin out so gradually that it is difficult to determine where the cartilage ends and the fibrous tissue begins.

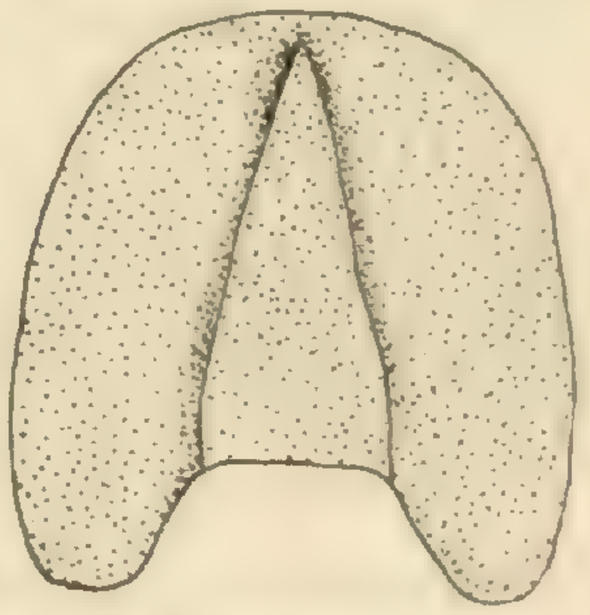


FIG. 9.—Dorsal view of the sternum.

The *coracoids*, which are described by Osawa as being composed of two parts, the procoracoids (Fig. 10, *P. C.*) and the coracoids (*C.*) proper, though there is nothing to distinguish the two regions, are by far the most conspicuous elements of the shoulder girdle. They are composed entirely of cartilage and, together with the sternum, form a complete, though thin cartilaginous sheath for the ventral side of the thoracic region of the body. They overlap each other almost completely, as each sheet extends almost to the opposite side of the body. Like the sternum the coracoid is very thin, especially at the edges, but, unlike the sternum, it has no thickening on either side for muscular or connective tissue attachments. At the outer edge the coracoid becomes considerably thickened, where it articulates with the scapular and with the humerus. With the scapula it is firmly united, but with the humerus it forms a ball-and-socket joint, the glenoid cavity (Fig.

10, *Gl.*) being rather deep to receive the rounded head (*H'.*) of the humerus (*H.*). The center of the coracoid is perforated by an irregular aperture of varying size (*F.*), called by Osawa the "supracoracoid foramen."

The *scapula* and *suprascapula* (Fig. 10, *Sc.*, *S. Sc.*) form, together, a spatula-shaped structure whose area is small in comparison with that of the coracoid, with which it is firmly united. The suprascapula forms the blade of the spatula, and is a broad, thin sheet of cartilage, somewhat curved to conform to the curvature of the side and back of the animal's body. The scapula is

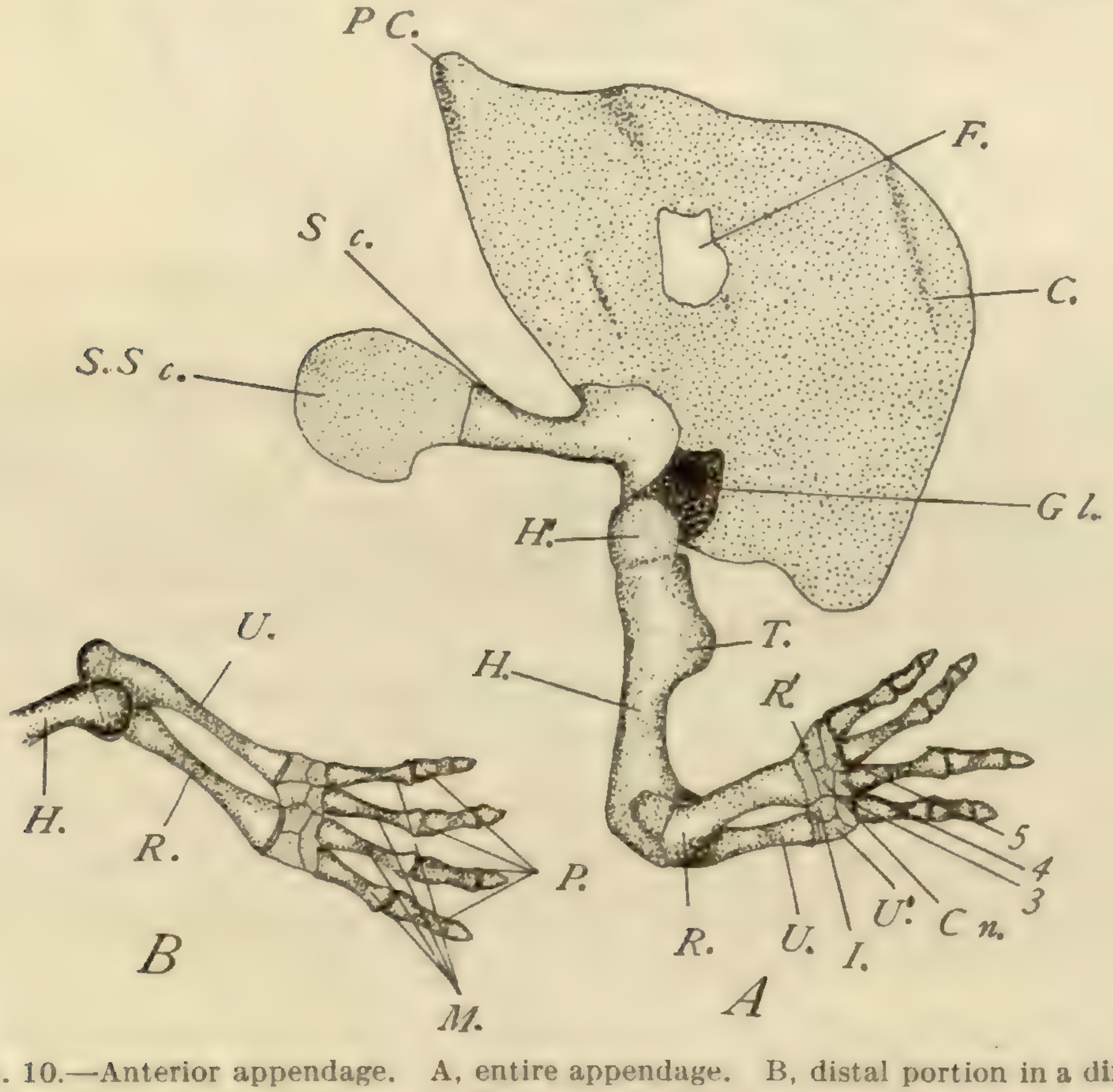


FIG. 10.—Anterior appendage. A, entire appendage. B, distal portion in a different position. *C.*, coracoid; *Cn.*, centrale; *F.*, foramen; *Gl.*, glenoid cavity; *H.*, humerus; *H'.*, head of humerus; *I.*, intermedium; *M.*, metacarpals; *P.*, phalanges; P. C., procoracoid; *R.*, radius; *R'.*, radiale; *Sc.*, scapula; *S. Sc.*, suprascapula; *T.*, tuberosity of humerus; *U.*, ulna; *U'.*, ulnare; *3*, *4*, *5*, distal row of carpals.

an elongated, somewhat flattened structure, slightly enlarged at one end, where it is attached to the suprascapula, and considerably enlarged at the other, where it is attached to the coracoid. It is the only part of the shoulder girdle that is composed of bone.

The *humerus* (Fig. 10, *H.*) is rather thick in proportion to its

length, and articulates with the glenoid cavity of the coracoid by the round, cartilaginous head (*H'*.). Its more or less cylindrical shaft is marked by a large tuberosity (*T*.) near its proximal end, and is separated from the head by a well marked neck. At its distal end it is broad, somewhat as in the human humerus, and articulates with both the radius and the ulna.

The *radius* and the *ulna* are entirely distinct from each other, and take nearly equal parts in the formation of both elbow and wrist joints, though the ulna, as is usual, is the more closely associated with the humerus. The ulna (Fig. 10, *U*.) is slightly longer than the radius (*R*.), and strongly resembles the corresponding bone in the human arm, though it is, of course, not so long in proportion to its diameter, and its shaft is not so nearly cylindrical in section. Its proximal end is enlarged to form the concave articular surface, the sigmoid cavity, and its distal end is also slightly enlarged, and is provided with a disc of cartilage of considerable thickness. The radius presents no peculiarities in structure. It enlarges rather rapidly from the center towards each end, where well marked discs of cartilage are found.

The *carpus*, though composed entirely of cartilage, shows with considerable distinctness the seven elements of which it is made up. Two elements articulate with each of the forearm bones: on the radial side are the radiale (*R'*.) and the centrale (*Cn*.), the latter lying in about the center of the carpus; on the ulnar side are the ulnare (*U'*.) and the intermedium (*I*.) Uniting the four elements above described with the metacarpals are three distal carpals (Fig. 10, *3*, *4*, *5*), one of which is united with two of the metacarpals. On the anterior appendage are four digits, each of which is made up of an elongated metacarpal element (*M*.) and two short phalangeal elements (*P*.), of which the more distal tapers to an almost claw-like sharpness. The two middle digits which are of about the same length, are somewhat longer than the two outer ones. There is no sign, on the fourth digit, of the third phalangeal element described by Osawa in the Japanese salamander. The relative sizes of the metacarpal and phalangeal elements are about the same in each of the four digits.

The Posterior Extremity.—The posterior extremity, consisting of the pelvic girdle and the hind legs, is a rather curious mixture

of cartilage and bone. Its structure, in general, agrees closely with the corresponding region in the Japanese species, as described by Osawa, except in regard to the epipubis, which is markedly different.

The *pelvic girdle* will first be described. Taken as a whole, it has a roughly triangular form. The apex is formed by the anteriorly directed epipubis, while the basal angles are formed by the dorso-posteriorly directed ilia. Its ventral surface is somewhat convex, and, along its posterior half, is marked by a slight, median, longitudinal ridge for the attachment of muscles. Its dorsal surface is concave, with the most marked concavity between the bases of the two ilia (Fig. 11). The greater part of the pelvis is made up of the pubis, which is divided into two parts, the pubis proper, and the epipubis.

The *pubis* proper is a shield-shaped plate of cartilage (Fig. 11, *P.*), whose ventral convexity and dorsal concavity have been mentioned in speaking of the pelvis as a whole. It is almost completely divided into lateral halves by a median suture which is especially evident at the posterior end of the pelvis, between the two ischia (Fig. 11, *S.*). On each side of this suture, slightly anterior to the middle region, there is a small opening (Fig. 11, *O. F.*), the obturator foramen. The posterior corners of the pubis are elevated for the attachment of the ilia (*I.*), and under these elevations the deep, well developed acetabula are situated.

Anteriorly, the pubis is prolonged into a long, cartilaginous *epipubis* (*Ep.*), which, instead of being forked as in the Japanese salamander and some other Amphibia, is a straight rod, slightly broadened and flattened at its distal end and somewhat enlarged both laterally and dorso-ventrally at its attached end. The union of the pubis and epipubis is a close one, but allows considerable freedom of motion.

Firmly united with the posterior end of the pubis, and continuous with it, are two oblong plates of bone, the *ischia* (*Is.*). Together, the ischia form a blunt, posteriorly projecting process to the pelvis. The ischia are separated along the middle line by the median suture, but their adjacent edges are not quite parallel, so that a slight cartilage-filled space is left between them at one place. There is also a small triangular piece of cartilage at their extreme posterior end.

The *ilia* (*I.*), like the ischia, are of bony consistency, except at their extremities, where there is a small amount of cartilage. They are somewhat curved in a postero-dorsal direction, and are considerably enlarged at their pelvic end, and less so at their sacral end.

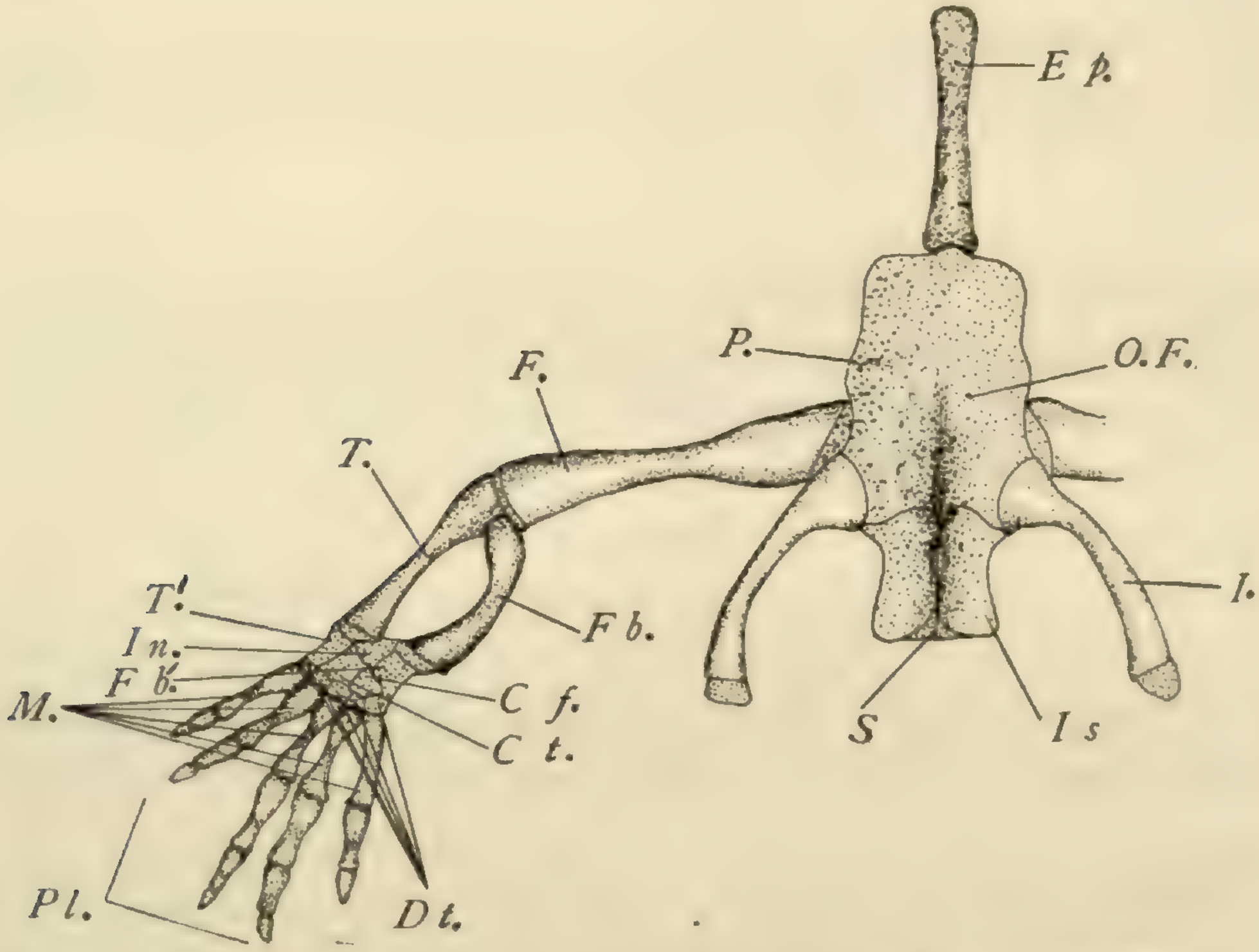


FIG. 11.—Posterior appendage, from the dorsal aspect. *Cf.*, centrale fibulare; *Ct.*, centrale tibialis; *Dt.*, distal row of tarsal elements; *Ep.*, epipubis; *F.*, femur; *Fb.*, fibula; *Fb'.*, fibulare; *I.*, ilium; *In.*, intermedium; *Is.*, ischium; *M.*, metatarsus; *Of.*, obturator foramen; *P.*, pubis; *Pl.*, phalanges; *S.*, suture; *T.*, tibia; *T.'*, tibiale.

The *femur* (Fig. 11, *F.*) is rather more slender in proportion to its length than it is in the Japanese animal. Its proximal end is enlarged to form a round, cartilaginous head, which articulates with the deep acetabular cavity that has already been mentioned. On the ventral side, near the proximal end, is a sort of trochanter, or roughened projection for the attachment of muscles. The shaft tapers rapidly from the enlarged proximal end to about the middle length of the bone, where it is nearly cylindrical in cross section, and is not more than half the diameter of the head. The distal half of the femur is much broadened, in a dorso-ventral direction, and flattened in an antero-posterior direction. This marked flattening does not show in the figure because of the posi-

tion in which the leg is drawn. This distal enlargement of the femur is slightly convex on its anterior surface, and concave on its posterior surface. On the convex anterior surface is a very slight ridge, which is prolonged distally as an inconspicuous knob. Almost the entire distal end of the femur articulates with the tibia, but there is a small articular surface for the proximal end of the fibula. Between the distal end of the femur and the proximal ends of the tibia and fibula is a layer of cartilage of considerable thickness.

The lower leg is made up of two entirely distinct bones, the tibia and fibula. Of these bones, the tibia (Fig. 11, *T.*) is larger and will be described first. It is considerably larger at its proximal than at its distal end, and forms almost the entire articular surface of the knee-joint. The proximal end is broadened and flattened in the same planes as is the distal end of the femur, with which it articulates. On the anterior surface of this end is a slight ridge, corresponding to the ridge that has been noted on the distal end of the femur. The shaft of the tibia tapers rapidly from the proximal end to a point a little beyond the middle of the bone, and then increases in size to form the somewhat flattened distal enlargement, which articulates with the tibiale and centrale of the foot. The flattening of the distal end is in the same plane as that of the more enlarged proximal end. The distal, like the proximal end, is provided with a well developed plate of cartilage.

The *fibula* (Fig. 11, *Fb.*) is not so long as the tibia, and, as is shown slightly exaggerated in the figure, is strongly bowed on the tibial side. The side away from the tibia is only slightly bent, so that the bow is chiefly due to the shape of the surface next to the tibia. The enlargement at the proximal end is rounded, and articulates laterally with the side of the tibia and proximally with the distal end of the femur. The shaft of the bone is somewhat flattened, so that it is elliptical instead of circular in cross section. The distal end is more enlarged than the proximal, but is flattened instead of being rounded. At the extreme end of each flattened surface is an inconspicuous depression, not shown in the figure. The fibula, like most of the other bones that have been described, ends, both proximally and distally, in cartilage.

The *tarsus*, like that of the Japanese species, is composed of

ten cartilaginous elements, which are arranged in two more or less definite groups, the proximal and the distal, with two elements in an intermediate position. Articulating with the tibia, or rather with the cartilage that tips the distal end of the tibia, is the *tibiale*, (*T'*.) an irregular, elongated mass of cartilage. Attached in the same way to the fibula is the *fibulare* (*Fb.'*); and lying in an intermediate position and articulating more or less with tibia, fibula, tibiale, and fibulare is the angular *intermedium* (*In.*). The distal row of tarsal elements (*Dt.*) is composed of five masses of cartilage, all of about the same size, and each attached to the basal end of one of the metatarsal bones. These distal cartilages are smaller than the proximal. Between the proximal and the distal rows, are two small elements (sometimes fused into one) called by Osawa the "*centrale tibiale*" and "*centrale fibulare*" (*Ct.* and *Cf.*).

The *metatarsus* (*M.*) is composed of five elongated, cylindrical bones, somewhat enlarged as usual at the ends. They are of nearly the same length, though the first (on the tibial side) is somewhat shorter than the rest, and the third and fourth are somewhat longer.

The *phalanges* (*Pl.*) of the first, second, and fifth digits are made up of two elements, while those of the third and fourth digits contain three elements each. The terminal element of each digit is a pointed, claw-like structure.

The Vascular System

For the purpose of working out the course of the blood vessels the usual method of injecting the arterial and venous systems with masses of different colors was used. The injection of the arterial system was accomplished with but little difficulty by inserting the cannula into the well developed conus arteriosus, and through it forcing the injection mass into all of the arteries. But the injection of the veins was a more difficult matter, and will be described in connection with the description of those vessels.

The Arterial System

From the anterior edge of the ventricle leads forward the thick-walled conus arteriosus (Fig. 12, *T.*). It is of considerable length, and is more or less bent towards the right. It becomes considerably enlarged anteriorly to form the conspicuous bulbus arteriosus (*B.*). The bulbus arteriosus gives off from its anterior end, on each side, four branchial vessels (Fig. 12, *1*, *2*, *3*, *4*), which diverge slightly as they pass towards the side. All four of these arches are united with one another, just beyond the gill cleft (*G. C.*). but it is from the second and third that the real systemic arch (*S.*), is chiefly formed. This complicated arrangement of the branchial blood vessels is, in the main, similar to that described in the Japanese hellbender by Osawa, but differs considerably from the description given by Chapman ('93), also of the Japanese salamander.

The first arch, which may be called the *carotid*, extends for some distance as a single vessel and then becomes slightly swollen to form a sort of *carotid gland* (*C. G.*), similar to that found in the frog. From the median side of the carotid gland is given off an artery which is distributed to the hyoid apparatus and the floor of the mouth, and may hence be called the *lingual* (*L.*).

Just beyond the carotid gland the arch divides and reunites again, giving off one or two small vessels to the neighboring parts. Then, after continuing for some distance as a single vessel, it divides into two vessels, the *external* and *internal carotids* (*E. C.*, *I.*). Just before dividing into the external and internal carotids the arch is connected with the main systemic arch by a vessel that is called by Marshall the ductus Botalli, by Osawa the ramus communicans (*Com.*).

The *second* and *third branchial arches* (Fig. 12, *2*, *3*), after running more or less parallel to each other to a point back of the carotid gland, unite to form the main *systemic arch* (*S.*). The third arch runs along the anterior margin of the gill cleft (*G. C.*), and gives off, just before uniting with the second arch, a branch to the fourth branchial arch. This branch may be called the ductus Botalli (*D. B.*).

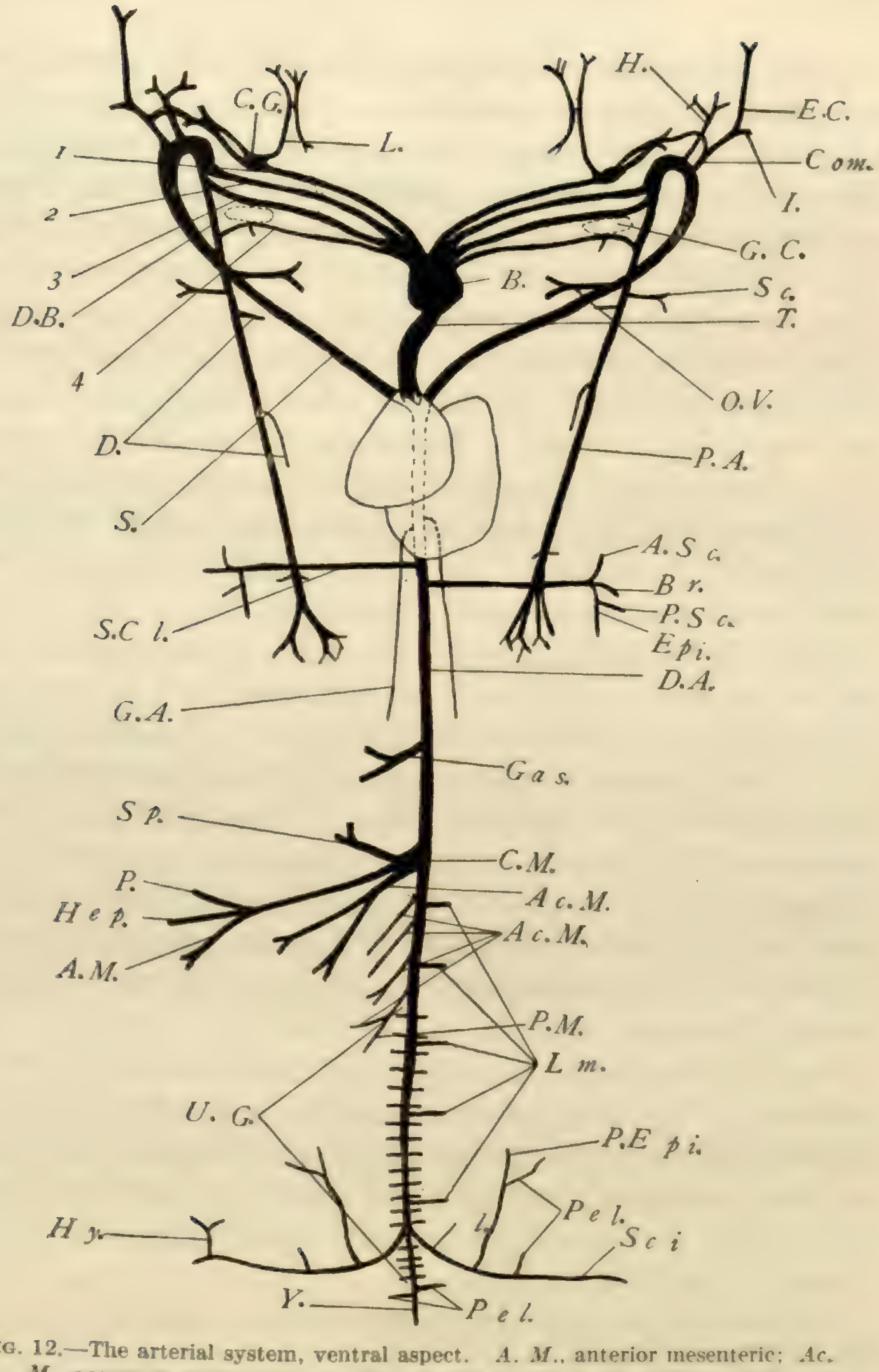


FIG. 12.—The arterial system, ventral aspect. *A. M.*, anterior mesenteric; *Ac. M.*, accessory mesenteric; *A. Sc.*, anterior scapular; *B.*, bulbus arteriosus; *Br.*, brachial; *C. G.*, carotid gland; *C. M.*, cœliaco-mesenteric; *Com.*, ramus communicans; *D.*, to dorsal region, near lungs; *D. A.*, dorsal aorta; *D. B.*, ductus Botalli; *E. C.*, external carotid; *Epi.*, epigastric; *G. A.*, anterior genital; *Gas.*, gastric; *G. C.*, gill cleft; *H.*, hyoid; *Hep.*, hepatic; *Hy.*, hypogastric; *I.*, internal carotid; *Il.*, iliac; *L.*, lingual; *Lm.*, lumbar; *O. V.*, occipito-vertebral; *P.*, pancreatic; *P. A.*, pulmonary; *Pel.*, pelvic; *P. Epi.*, posterior epigastric; *P. M.*, posterior mesenteric; *P. Sc.*, posterior scapular; *S.*, systemic arch; *Sc.*, scapular; *Sci.*, sciatic; *S. Cl.*, subclavian; *Sp.*, splenic; *T.*, conus arteriosus; *U. G.*, urogenital; *Y.*, caudal; *1*, *2*, *3*, *4*, first to fourth branchial arches.

A short distance beyond the point of union of the second and third arches, the systemic arch gives off a well marked vessel (*H.*), to the end of the hyoid apparatus, and some distance beyond this it gives off an occipito-vertebral artery to the vertebral column and occipital region (*O. V.*). After passing around to the dorsal side of the digestive tract, the two systemic arches unite, just above the heart, to form the dorsal aorta (*D. A.*).

The *fourth branchial arch* passes just posterior to the gill opening, at the outer margin of which it is connected with the third arch by the ductus Botalli. Beyond the ductus Botalli it gives off an artery (*Sc.*) to the region of the scapula, and then two small arteries (*D.*) to the muscles of the dorsal part of the body in the region of the lungs. The main branch of this arch continues posteriorly as the pulmonary artery (*P. A.*).

Some variation in the relative sizes of the vessels of the branchial region occurs as well as some slight variation in their distribution, but the normal condition is about as described above.

The distribution of the blood vessels that arise as branches of the dorsal aorta will now be described. The aorta and its branches are so easily filled with the injection fluid that it is a comparatively easy matter to work out their distribution, especially in the abdominal region. In fact, the only part of the arterial system that offers any difficulty is the outer part of the visceral arches, in the region of the gill openings.

The branches of the aorta will be described in order from before backward. The most anterior branches are given off in the region of the heart, as a pair of rather small arteries (Fig. 12, *G. A.*) which arise nearly opposite each other and extend in a posterior direction to supply the anterior part of the reproductive organs, especially the oviducts.

A short distance posterior to the last described arteries, are given off the two *subclavians* (*S. Cl.*), the right vessel arising a little anterior to the left. As might be expected from the slight development of the anterior appendages, the subclavian arteries are comparatively small vessels. On reaching the shoulder girdle, each subclavian divides into four main branches. The most anterior of these (*A. Sc.*) supplies blood to the region in front of the scapula. The next branch (*Br.*) is the brachial, and extends

into the fore leg. The third branch (*P. Sc.*) extends to the region posterior to the scapula, and also probably, to the posterior border of the fore leg. The most posterior branch of the subclavian (*Epi.*) runs in a posterior direction, and carries blood to the lateral part of the body back of the anterior leg; it is called by Osawa the epigastric.

Some distance posterior to the subclavians is seen an unpaired vessel (*Gas.*) which sends branches to the lesser curvature of the stomach, and may be called the gastric. The next artery, which may be called the cœliaco-mesenteric (*C. M.*), is a rather large one, and branches almost immediately into three parts. The most anterior of these branches (*Sp.*) supplies the greater curvature of the stomach, and also the spleen, and may be called the splenic. The second branch of the cœliaco-mesenteric divides into three smaller branches: a pancreatic (*P.*) supplying the pancreas; a hepatic (*Hep.*) supplying the liver; and a third branch, the anterior mesenteric (*A. M.*), which carries blood to the anterior third of the small intestine.

The most posterior of the three branches of the cœliaco-mesenteric artery is distributed to the small intestine posterior to the region supplied by the anterior mesenteric; it is the first of several vessels that supply blood to the posterior two thirds of the small intestine, and that might be called accessory mesenterics (*Ac. M.*). There are three unpaired accessory mesenterics posterior to the one just described, and a fourth is formed as one of the two divisions of another unpaired branch of the dorsal aorta (*Ac. M.*). There are thus five of the so called accessory mesenteric arteries.

The artery (*P. M.*), with which the most posterior of the accessory mesenterics unites to form a single vessel is the posterior or inferior mesenteric and supplies blood to the anterior third of the large intestine. Five or six rather large, unpaired arteries (*Lm.*) are given off by the aorta, at more or less regular intervals, between the origin of the cœliaco-mesenteric and the iliacs. These lumbar arteries pass into the body wall along the mid-dorsal line.

Numerous pairs of urogenital arteries (*U. G.*) are given off by the aorta in the abdominal region, and supply the kidneys and reproductive organs. On account of the great elongation of the kidneys in a posterior direction, the last of the urogenital arteries

lie as far back as the cloaca or even posterior to it. In the neighborhood of the cloaca, the dorsal aorta gives off a pair of large arteries, the iliacs (*Il.*) which are continued into the posterior appendages as the sciatic arteries (*Sci.*). Each iliac artery gives off, a short distance from its origin, a vessel, the posterior epigastric (*P. Epi.*), which is chiefly distributed to the ventral body wall, but which also sends blood to the pelvic region (*Pel.*). A short distance distal to the posterior epigastric, each iliac gives off a small artery to the pelvic region. From the right iliac an additional artery is given off, distal to those just described, to the bladder and the posterior end of the rectum. This is the hypogastric (*Hy.*).

Posterior to the point of origin of the iliac arteries, the aorta continues backward, with diminished caliber, as the caudal artery (*Y.*) to supply blood to the tail. Besides several pairs of renal arteries, there is given off from the aorta, just back of the iliacs, a pair of arteries (*Pel.*), to supply blood to the dorsal region of the pelvis. This completes the description of the more important vessels of the arterial system. Without stopping to describe the distribution of the more minute vessels, the venous system will now be described.

The Venous System

The venous system is much more difficult to work out than the arterial system, due chiefly to the difficulty of obtaining good injections, especially in the region anterior to the heart.

The venous system, as described in this paper, will exhibit more differences from that described by Dr. Osawa for the Japanese giant salamander than were seen in connection with the arterial system. The veins of the posterior region of the body were injected, without especial difficulty, as follows: the abdominal vein was injected both forwards and backwards; the portal vein was injected forwards, beginning so far towards the tail that practically the entire system was filled; and the posterior vena cava was injected by cutting off the tail and inserting the cannula into the caudal vein. The veins of the anterior parts of the body were injected through the anterior venæ cavæ, and it was here

that the greatest difficulty was experienced in getting the injection fluid into the smaller vessels, in fact, it was only by repeated injections at various points that even the more important veins of this region could be filled. The posterior end of the posterior cardinal veins could not be filled with the injection mass, even after repeated attempts, so that the connections of these veins, if any exist, with the other veins of the abdominal region could not be made out.

The conspicuous, thin-walled *sinus venosus* (Figs. 13 and 14, *S. V.*) into which the blood from the various parts of the body is emptied, is formed mainly by the union of three large veins: the two superior venæ cavæ (*S. C.*), and the inferior vena cava (*I. C.*). The pulmonary veins (*L.*), bringing blood back to the heart from the lungs, as their name would indicate, unite with each other dorsal to the sinus venosus, and empty into the latter at a point whose exact location is difficult to determine on account of the small size of these pulmonary vessels. The superior vena cava of the right side seemed in most, if not all cases, to be attached to the apex of the ventricle. What the object of this attachment might be, was not determined. Each superior vena cava is formed by the union of the following veins: the innominate (*In.*) which is practically nothing more than the lateral continuation of the superior cava itself, the external jugular (*E. J.*), and the posterior cardinal (*Car.*).

The external jugular collects blood chiefly from the lower side of the head, and is formed by the union of two veins which probably correspond to the mandibular and lingual or laryngeal, though they could not be traced to their origin.

The posterior cardinal (*Car.*) empties into the superior cava at a point nearly opposite the opening of the external jugular. Throughout most of its course it lies deeply buried in the muscles of the dorsal body wall, and, as has been said, its extreme posterior termination could not be determined, owing to the impossibility of obtaining a complete injection. It was traced backward as far as the anterior end of the kidney, but whether beyond that point it is simply lost in the body wall or is connected with some of the veins of the abdominal region, could not be determined. Near its anterior termination the posterior cardinal is

joined by a vessel (*S.*) from the region of the shoulder, and a short distance posterior to this point it is connected, by a sort

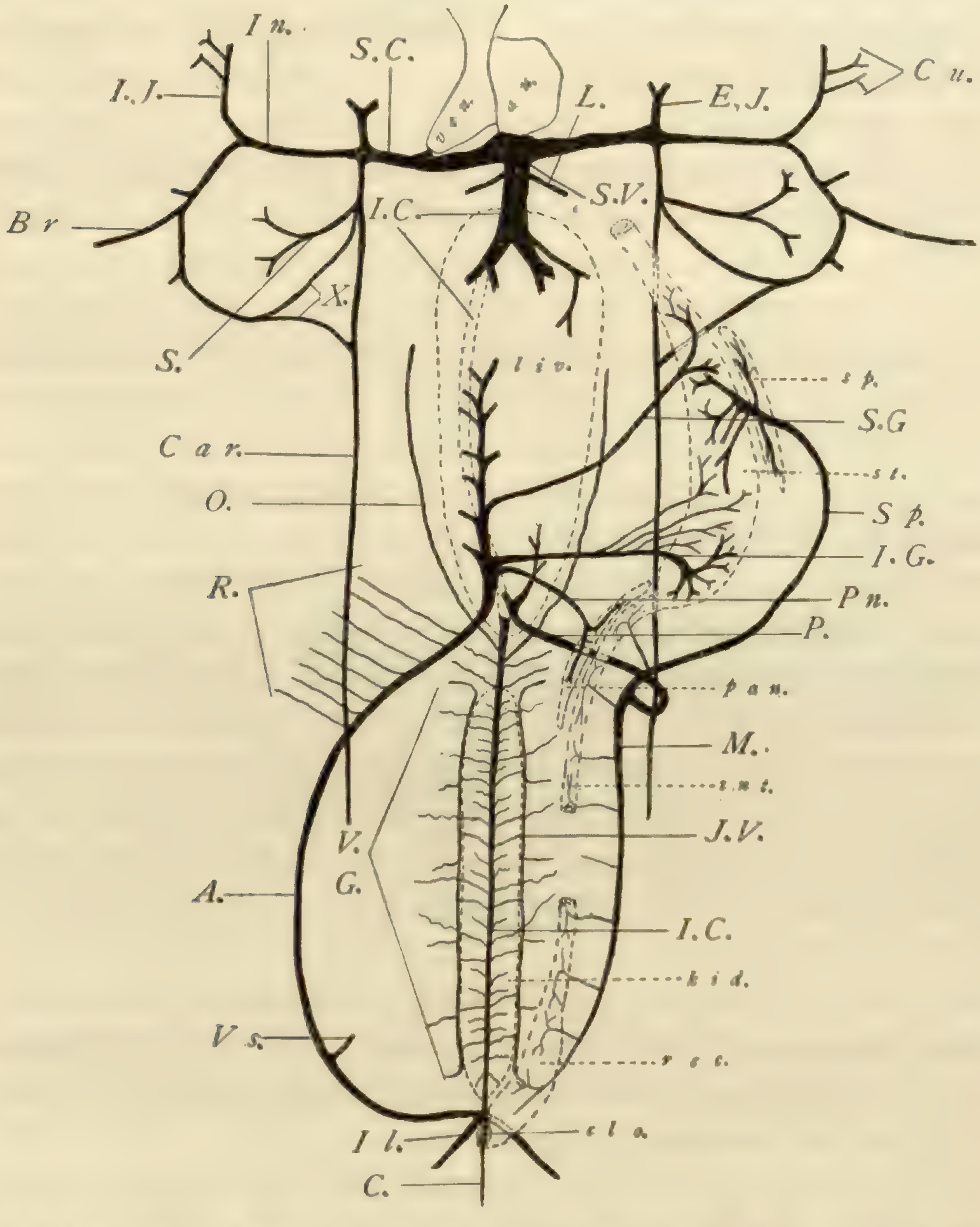


FIG. 13.—The venous system, ventral aspect. *A.*, abdominal; *Br.*, brachial; *C.*, caudal; *Car.*, posterior cardinal; *Cu.*, cutaneous; *E. J.*, external jugular; *G.*, genital; *I. C.*, inferior cava; *I. G.*, inferior gastric; *I. J.*, internal jugular; *Il.*, iliac; *In.*, innominate; *J. V.*, vein of Jacobson; *L.*, pulmonary; *M.*, mesenteric; *O.*, oviduct; *P.*, portal; *Pn.*, pancreatic; *R.*, parietals; *S. C.*, superior vena cava; *S.*, from shoulder; *Sp.*, splenic; *S. V.*, sinus venosus; *V.*, vertebral; *Vs.*, from urinary bladder; *X.*, plexus.

of simple plexus of veins (*X.*), with the brachial vein (*Br.*) which brings blood to the heart from the anterior appendage. To the brachial and to the plexus of veins just mentioned, are added a

number of small veins from the region of the shoulder. The innominate vein (*In.*) is formed by the union of the internal jugular (*I. J.*) and the brachial (*Br.*). The main branch of the former returns blood from the interior of the skull, and is joined shortly before its union with the brachial, by two smaller vessels (*Cu.*), leading from the side of the head. The brachial, as might be expected from the small size of the fore leg, is a comparatively small vein. This completes the description of the vessels connected with the superior venæ cavæ, as the vessels of the two sides of the body in this region are alike.

The veins of the abdominal region will now be described. Since these vessels are usually injected without difficulty, their distribution may be made out with comparative ease. One of the largest and most noticeable veins in the body is the *abdominal* (*A.*). It adheres closely to ventral body wall, slightly to the right of the median line, and, unless care be taken, may easily be cut in opening the abdominal cavity. In the diagram it, like the veins from the stomach and intestines, is for the sake of clearness drawn towards the side. Posteriorly it is formed chiefly by the union of the two iliac veins (*Il.*), a union which takes place just anterior to the cloaca (*clo.*). The iliac veins return the blood from the posterior appendages, and, like the brachial veins, are of comparatively small size. A short distance anterior to the point of union of the iliac veins the abdominal vein receives a very small vein (*Vs.*) from the urinary bladder. Into the most anterior quarter of the abdominal vein, near to its junction with the liver, empty several (eight or nine) veins, the parietals (*R.*), which return blood from the ventral body wall. Anteriorly, the abdominal vein enters the liver, a little in front of the apex, and becomes broken up into capillaries, though it may be traced along the ventral surface of the liver for a considerable distance in an anterior direction.

The arrangement of the veins from the stomach and intestines, the *hepatic-portal system*, is rather peculiar, and will now be described. The blood from practically the entire length of the intestines, both small and large, is collected by a single vein (*M.*) which may be called the mesenteric. A short distance posterior to the liver, this vein unites with the splenic vein (*Sp.*) to form the

main branch of the portal vein (*P.*) through which the blood finds its way into the liver. The splenic vein, as its name would indicate, collects blood from the spleen, but it brings blood also from the middle region of the stomach. The greater part of the blood from the stomach is collected into two well marked veins, the superior and inferior gastrics (*S. G.*, *I. G.*) which empty into that part of the abdominal vein which has already been described as extending for some distance along the ventral side of the liver. Of these two gastric veins, the inferior is the larger, and empties into the abdominal vein at some distance behind the superior gastric. Emptying into the abdominal at almost the same place with the inferior gastric, is a vein of considerable size, the pancreatic (*Pn.*). The portal vein proper, then, brings blood to the liver from the intestines and the spleen; but most of the blood from the stomach and apparently all that from the pancreas is carried into the liver through the abdominal vein.

It now remains only to describe the system of the *inferior vena cava*, and especially that part of the system that lies posterior to the liver. The blood from the tail is collected into a caudal vein (*C.*) that, after entering the abdominal cavity, becomes the inferior or posterior vena cava (*I. C.*). This posterior part of the inferior cava lies between and slightly ventral to the kidneys, and is so closely associated with these organs, from which it receives numerous veins, that its individuality as a distinct vessel seems almost lost. Extending along the distal sides of the kidneys, and connected at frequent intervals by small vessels with the inferior cava, are the more or less distinct veins of Jacobson (*J. V.*). Each vein of Jacobson receives about six vertebral veins (*V.*) from the corresponding side of the vertebral column. On account of the great number of the renal veins and the close attachment to the kidneys of the veins of Jacobson, the details of these veins are difficult to determine.

The blood from the reproductive organs is emptied into the inferior cava through several pairs of genital veins (*G.*), some of which lie anterior to the kidneys while some cross the anterior ends of these organs to reach the inferior cava. In the female, a comparatively large vein leads from the anterior end of each oviduct to empty into the inferior cava just behind the liver (*O.*).

The inferior cava enters the liver near the apex of the right lobe. By carefully dissecting away the substance of the liver, the course of this large vein may be followed entirely through that organ. It extends in a nearly straight line through the dorso-lateral part of the right lobe, and emerges from the anterior surface of the liver as the large thin-walled vessel that empties into the heart. Just before, or at about the time of its emergence from the liver, it is joined by the large hepatic vein, so that that part of the inferior vena cava which is anterior to the liver is many times as large as that part which is posterior to the liver. This completes the description of the more important peripheral vessels of the vascular system; and it now remains to describe the structure of the heart.

The Heart

The heart lies far forward in the body, just anterior to a line joining the front legs. It is protected ventrally by the broad underlying cartilages of the procoracoids and the sternum, to which it lies so close that they must be removed with some care in order not to cut into the pericardial cavity. The size of the heart is moderate in relation to the size of the entire animal, and seems to vary considerably, even in animals of the same approximate size. It has the vitality usually seen in cold-blooded animals, and will continue to beat for a considerable time after being removed from the body, or after being filled with the injection fluid.

External Anatomy.— When seen from the ventral aspect (Fig. 14, A), it presents six main regions: the conus arteriosus, the bulbus arteriosus, the ventricle, the right and left atria or auricles, and the sinus venosus. These regions may be seen from the dorsal aspect as well, if the heart be dissected from the body (Fig. 14, B), and they will now be described in turn. Their form and relative size will vary somewhat, of course, with their state of distension at the time they are sketched. The heart from which the figure was made, was moderately well filled with the injection fluid, and differs considerably in general appearance from Osawa's figures of the heart of the Japanese salamander.

The bulbus arteriosus (*B.*), to begin at the most anterior region of the heart, is a striking object, seen on removing the skin and the

cartilages of the pectoral girdle from the ventral side of the throat. It is of a whitish color, and its walls are tough and thick. Anteriorly it divides to form the arterial arches of each side, and posteriorly it narrows suddenly to form the truncus, which connects with it at somewhat of an angle, instead of entering exactly in the middle line. Its ventral surface is smooth and even, while its dorsal surface may be more or less grooved longitudinally, as seen in the figure. In cross section it is elliptical, and is compressed in a dorso-ventral direction.

The conus arteriosus (*C.*) is a well marked tubular structure

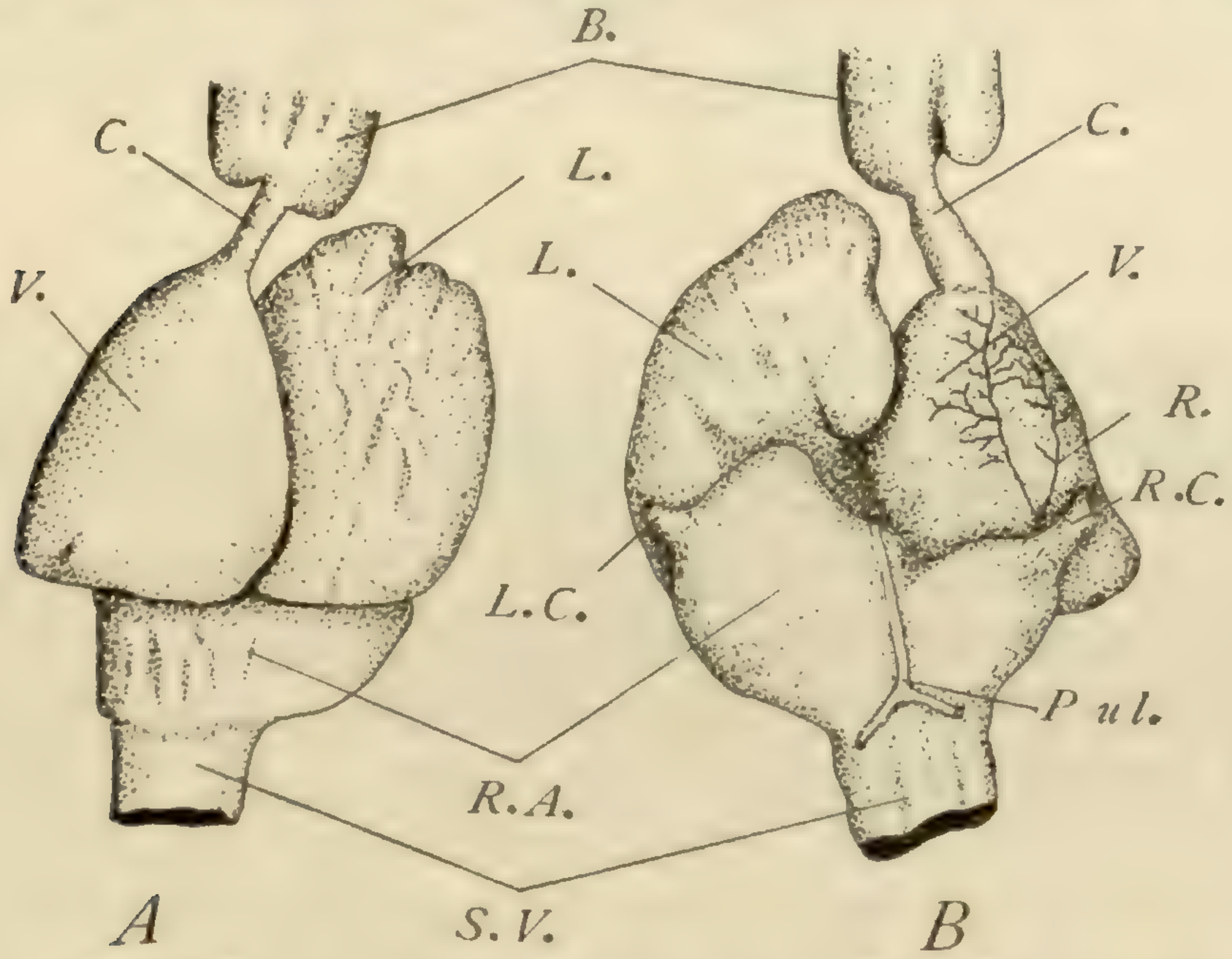


Fig. 14.—The heart. A, ventral. B, dorsal aspect. *B.*, bulbus arteriosus; *C.*, conus arteriosus; *L.*, left auricle; *L. C.*, left anterior vena cava; *Pul.*, pulmonary; *R.*, coronary vessels; *R. C.*, right anterior vena cava; *S. V.*, sinus venosus; V., ventricle.

leading from the anterior angle of the ventricle, and becoming enlarged at its anterior end to form the bulbus arteriosus that has just been described. It is unusually long, and its cylindrical shape and tough walls make it an excellent place into which to insert a cannula for the purpose of injecting the arterial system.

The ventricle (*V.*) is a thick-walled structure of a markedly triangular form, especially when seen from the ventral side (Fig. 14, A), with the apex of the triangle towards the head, where it opens into the truncus arteriosus. Owing to the thick muscular walls the ventricle remains smooth and of about the same size and shape

whether it be empty or distended. It forms the right anterior quarter of the heart, and lies somewhat ventral to the other parts of that organ.

The left auricle or atrium (*L.*) forms the left anterior quarter of the heart, and is its largest division, though on account of its thin distensible walls this chamber may vary considerably in size. Its walls are usually wrinkled and uneven, and its outline is more rounded than that of the ventricle, though the entire outline cannot be seen in either a dorsal or a ventral view, since the chamber is partially covered dorsally by the left auricle, and ventrally by the ventricle. At some point on its dorsal side the vein (*Pul.*) formed by the union of the two pulmonary veins probably enters it, but, on account of the very small size of this single pulmonary vein, its exact point of entrance could not be determined with certainty, and so has not been indicated in the figure. The size of the pulmonary veins in the figure has been exaggerated. The anterior edge of the left auricle lies nearer the head than any other part of the heart except the bulbus arteriosus.

The right auricle (*R. A.*) lies dorsal and posterior to the ventricle and the left auricle, so that in a ventral view of the heart only the posterior half of this chamber shows. Owing to its very thin walls and to the large opening of the sinus venosus it has no very definite shape. It is depressed in a dorso-ventral direction, and its greatest diameter is from side to side. Into its antero-lateral corners open the right and left anterior venæ cavæ (*R. C.*, *L. C.*), while posteriorly it is separated by only a slight constriction, externally, from the sinus venosus which in turn is continued back as the posterior vena cava. Extending longitudinally across the dorsal wall of the right auricle, and closely attached to it, is the pulmonary vein (*Pul.*), formed by the union of the two small veins from the lungs.

The sinus venosus (*S. V.*) is merely the enlarged anterior end of the posterior or inferior vena cava. Its walls are extremely thin, and its size and shape will depend upon the amount of fluid it contains. Blood vessels to supply the walls of the heart may be seen at several places, and are shown in the figure at *R*.

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CONTENTS

			Page
I.	Application of de Vries's Mutation Theory to the Mollusca	F. C. BAKER	327
II.	Notes on the Genus Leptophrys	W. A. KEPNER	335
III.	Egg-laying of Crayfish	DR. E. A. ANDREWS	343
IV.	Sowerby's Whale on the American Coast	DR. G. M. ALLEN	357
V.	Fresh-water Rhizopods of Nantucket	J. A. CUSHMAN	371
VI.	Notes and Literature: *Zoölogy*, Weismann's Theory of Descent, Brooks's The Oyster, Mayer's Sea-shore Life, Alder and Hancock's British Tunicata, Schillings's With Flash-light and Rifle, Notes, *Recent Extension of the Range of the Green Crab* (O. Bryant), Ichthyological Notes		375

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APPLICATION OF DE VRIES'S MUTATION THEORY TO THE MOLLUSCA

FRANK COLLINS BAKER

PROBABLY no work since the publication of Darwin's *Origin of Species* has produced such a profound sensation in the biological world as the work entitled *Die Mutationstheorie*, by Hugo de Vries. A perusal of that work (or, perhaps better for those not having the time, the shorter work *Species and Varieties; their Origin by Mutation*) leads the zoölogist to ponder upon the question as to how far these theories may be used in connection with animal forms, especially with the invertebrates. Much experimentation, covering a long period of time, must be done, however, before anything definite can be accomplished. De Vries spent twenty years raising and studying primroses. The zoölogist must do likewise and study some common forms for a long period, breeding them under conditions conforming as closely as possible to the natural environments of the organisms. The question of elementary species and varieties is one which would seem to have a meaning in botany somewhat different from the use of the same terms in zoölogy, in fact, in some of the Invertebrata (the Mollusca, for example) there would seem to be no distinction between an elementary species and a variety, the terms being synonymous. However this may be, it would seem that to the Mollusca the de Vries theory might be applied with some interesting results. The writer would ask the question: Are not many of the variations of the Mollusca produced in the manner outlined by this new aspect of evolution? The writer does not feel warranted

in answering this question in the affirmative, but he does believe that the illustrations which follow are suggestive and certainly point to some such derivation. It is not held, even by de Vries, I take it, that the mutation theory is to supplant or take the place of the older evolution by whose slow and gradual processes (natural selection, survival, environment, distribution, etc.) the present state of animal and vegetal matter has been reached, but as an additional process in that great scheme of life.

In certain mollusks the species seem to be unstable, that is, they have a tendency to vary, not in a given direction but in many

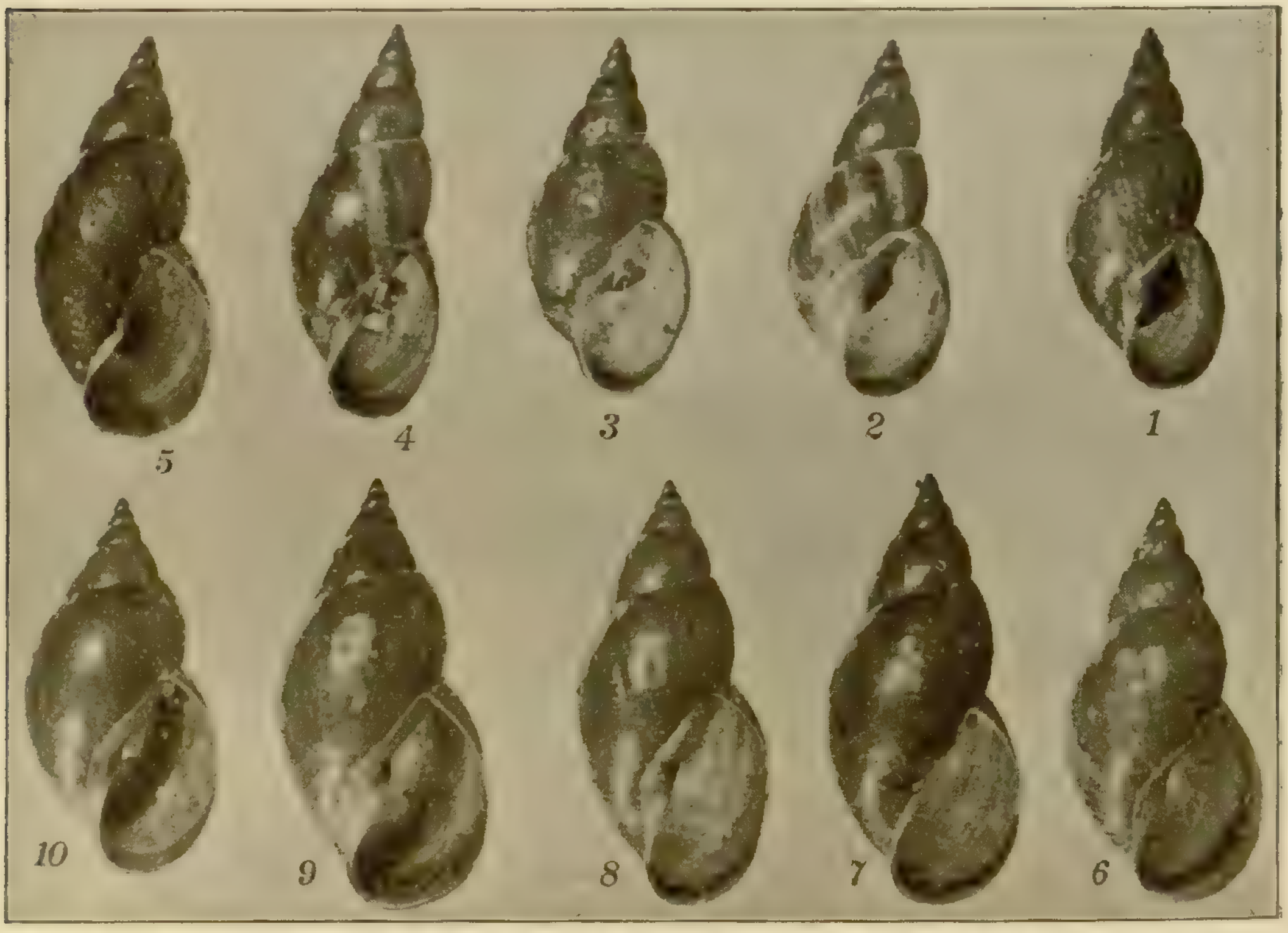


FIG. 1.— *Lymnæa palustris* Müller, from Halma, Minnesota. Note the wide range of variation in the form of the shell. Enlarged.

directions at the same time. These seem to come under the head of mutants, or sports. The fresh-water pulmonates belonging to the genus Lymnæa are examples of this class and every species which has been studied in any quantity has been found to vary in this manner. *Lymnæa palustris* Müller (= *elodes* Say) is one of the most notably variable, and its mutations are many and marked. Fig. 1 represents a set of ten shells of this species collected by Mr. L. E. Daniels in Muskag swamps, Halma, Minnesota. They vary from a long, narrow shell, with elevated spire

(1) to a fat, robust shell, with a comparatively short spire (10). In some specimens the whorls are flat-sided (4), while in others they are convex, especially the last, which is very convex (3, 10). The columella plait also varies in size and elevation and the sutures vary in the degree of impression (compare 3, 4). Several of these mutations, if we can so designate these variations, have

FIG. 2.— *Lymnæa palustris* Müller, from Sugar Island, Alpena, Michigan. Enlarged.

been described as species or varieties; thus 10 is Lea's *nuttalliana* and 1 is Say's *elodes*. It will be seen that no line can be drawn between 1 and 10 in the presence of the intervening figures. Take away these connecting links and a very distinct variety remains.

In the Mollusca the factor of geographic variation plays a very important part. The shells from the locality illustrated in Fig. 1 are rather small, measuring 23 mm. in length. Fig. 2 illustrates the same species from Sugar Island, near Alpena, Michigan (col-

lected by Dr. W. A. Nason); the shells are much larger than those of Fig. 1, and measure 30 mm. in length. It will also be noted that the variation in this lot of shells is not so marked as in those illustrated in Fig. 1. There is considerable difference between the extremes but the majority of specimens conform more or less to a single type, the large, corpulent form. A study of several hundred specimens from each locality shows that each lot varies a certain percentage toward a given form. In lot 1, (Fig. 1), the variation is 75 percent toward no. 1, while in lot 2 (Fig. 2) the variation is about 60 percent toward no. 8. Without more data to disprove it, this would seem to point to the fact that the species of each locality varies toward a definite form. In lot no. 1 the dominant form is *palustris*, while in lot no. 2 the dominant form is *nuttalliana*.

The interesting fact in connection with all this is (and this is where de Vries's mutation theory seems applicable) that all the forms illustrated will develop from the same egg capsule. The eggs laid by *nuttalliana* will produce narrow *palustris* as well as the fat parent form, while the narrowest *palustris* will likewise produce the fattest *nuttalliana*. May this not be an illustration, also, of two types (although this subject is treated under ever-sporting varieties by de Vries) which he calls poor races and rich races. In Fig. 1, 75 percent of the progeny are *palustris* (assuming that the parent was a *palustris* form) and are of the rich race, while in Fig. 2 (assuming the parent to be *palustris*) the progeny are of the poor form, only 40 percent being the *palustris* form. This, however, is only hypothetical in this case. Nothing but actual experimentation can give accuracy to this phase of the subject.

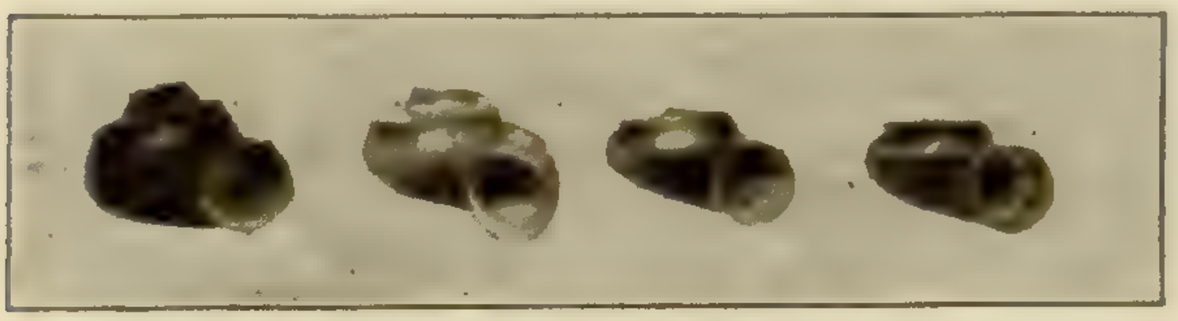


FIG. 3.—Variation in Valvata. 1. *V. tricarinata* Say. 2. *V. tricarinata confusa* Walker. 3. *V. bicarinata* Lea. 4. *V. bicarinata normalis* Walker. All enlarged.

In some other groups of shells the variation is along certain definite lines and the species seem to be more stable. For example, among the land shells *Polygyra profunda* and *Polygyra multilineata* vary in lacking or having bands, the uniform varieties being light (albino) or dark. *Polygyra tridentata* varies in its aperture

from no teeth through one, two, to three teeth. Some of the forms of Polygyra may be perforate or imperforate (*Polygyra monodon*, for example). In Valvata (Fig. 3) the variation seems to be still more marked, the variant being in the number and position of the carinæ; for example, *Valvata tricarinata* has three carinæ (1); var. *confusa* has two carinæ (2) and another variety has one carina. So also with *Valvata bicarinata*, which has two carinæ (3) while the variety *normalis* has three carinæ (4). *Vivipara contectoides* is another example in point, the typical form being banded, while a variety is without bands. These variations would seem to conform to de Vries's retrograde varieties, differing from the parent species in the absence of one or two characters. The majority of the latter examples are true varieties, lacking some characteristics of the type form, while the variations of Lymnæa are mutations combining most of the characteristics of the parent form. It is to be noted, however, that these two conditions overlap each other, so that no sharp and fast line can be drawn between them.

Some of the paleontologists have hailed de Vries's theory with delight, for they say that it is only in the light of such a theory that the sudden appearance of marked types in certain ancient faunas becomes intelligible. May it not also account for the finding of certain new species in regions supposed to have been thoroughly explored? May it not also account for the sudden disappearance of certain species, the mutations dying out but the parent form still continuing? A case in point is *Lymnæa shurtleffi* described from an artificial pond at Weatogue, Hartford Co., Connecticut. This species was found in large numbers, together with a new variety of Planorbis (*P. circumstriatus* Tryon). The finding of this Lymnæa is thus described by Mr. Tryon:[1] —

"The circumstances under which this and the following species were found are so peculiar that it is with great hesitation that I have ventured on a description of either of them. That new species of these shells should exist undetected in sections of the United States which have been so well explored by assiduous naturalists would be surprising; but in the present instance the almost irresistible supposition is, *that these species are of very*

[1] *Amer. Journ. Conch.*, vol. 2, p. 112, 1866.

recent origin [italics mine] in fact, *contemporaneous with that of the body of water which they inhabit.* I have looked in vain for some evidence upon the specimens themselves of the effect of some strong local influence. The species are so distinct that they afford no clew to a possible derivation from others.

"In conclusion, I present the following interesting particulars:

"Extract from a letter from the late Dr. S. Shurtleff to Isaac Lea, Esq., Weatogue, Hartford Co., Connecticut, November 22, 1865.

"In the summer of 1860 I made an excavation some two rods below a spring that flows about eight months in the year. The spring comes from a neighboring hill. The overlying rock is New Red Sandstone. From the time of the excavation till the summer of 1864 there was water in the artificial pond. It was dry in 1864, but I did not examine for shells, as before the excavation I had repeatedly examined the spring, but never found shells of any description.

"After my return from Pennsylvania, in September, 1865, accidentally crossing the pond, which was dry, I noticed quantities of shells clustered in the hollows. I gathered a few and laid them by for leisure examination; when I came to look at them again I found *L. umbrosa,* as I supposed, as well as a non descript species. I immediately went to the pond and secured all the Lymnæans I could find— some alive and many dead; and, fearing the dry season would destroy them all, I put many of the living shells into a pond that I have since made, that will never dry up. I may have collected 50 specimens of *L. umbrosa* (?) and of other specimens a half-pint.

"How these shells came into the pond is as much a matter of surprise to me as it is to you. I have no knowledge that there was ever a shell put into the pond.

"One fact more. The spring and pond are perfectly isolated, as the overflow disappears at the edge of a sandy plain in less than ten rods from its fountain head, and there is no stream of perpetual running water within one mile of it. The Farmington River is about a mile distant in the valley below, and here the only species yet found are *Lymnæa columella* Say, *Physa heterostropha* Say, *Planorbis bicarinatus* Say, *Vivipara decisa* Say, *Unio complanatus* Solander, and *Unio radiatus* Lamarck.

"The pond is two hundred feet above the bed of Farmington River."

Tryon says: "Besides the above two species I found a single specimen of *Lymnæa umbrosa* Say, and several of *L. desidiosa* Say."

From the foregoing account it would appear that *shurtleffi* (Fig. 4) was an offshoot (or mutant, if we apply the de Vries theory) of *umbrosa*[1] (= *elodes* = *palustris*), that being the only other species present (save *desidiosa*, which belongs to quite another group of Lymnæas). It may be thought by some that *shurtleffi* might have been produced by unfavorable conditions, but as the shells, one of the original lot of which was recently examined by the writer, are perfect and not distorted, this could hardly have been the case. All the evidence points to the conclusion that *shurtleffi* is a new species evolved or given off from *palustris*. The short, acute spire, subcylindrical, compressed body whorl, the partly open umbilicus, and the long and narrow aperture are the principal characteristics of the new species.

FIG. 4.— *Lymnæa shurtleffi* Tryon. Cotype. From Weatogue, Connecticut. Enlarged.

The foregoing remarks are not made with the idea of fastening the mutation theory upon the Mollusca, but only to call attention to these apparently analogous cases of mutation and variation to the end that other zoölogists may take up the matter and by experimentation and by the study of abundant material from various localities gather a large amount of data bearing upon this theory as applied to the Mollusca.

While the mutation theory seems to fit in very nicely in explaining the very large amount of variation in the fresh-water pulmonates, we must not be too hasty in applying this new theory, founded as it is upon plant variation, to animal life. Dr. J. A. Allen, in a

[1] *Umbrosa* is placed by some conchologists in the synonymy of *reflexa*. I have examined the type specimens in the Philadelphia Academy and they are good examples of *elodes*.

recent number of *Science*[1] calls attention to the danger of accepting this hypothesis without more conclusive proof, and I cannot do better than to close this communication with his remarks. He says: "While the mutation theory may be a good hypothesis to consider in respect to these peculiarly unstable groups of birds, it must be noted that the method of their origin and the results, as now known, are very unlike the methods and results of mutation in plants, as made known by de Vries. The facts and conditions are not to any great extent parallel. Instead of the resultant 'mutants' remaining constant and breeding true, as in the case of primroses, they are in this case unstable and are believed to interbreed freely with each other and the parent stock."

I am indebted to the following gentlemen for assistance in the preparation of this paper: Dr. Henry A. Pilsbry, Academy of Natural Sciences, Philadelphia, Pa., for the loan of a type specimen of *Lymnæa shurtleffi*; Mr. L. E. Daniels, La Porte, Indiana, for specimens of *L. palustris* from Minnesota; Dr. W. A. Nason, Algonquin, Illinois, for specimens of *L. palustris* from Michigan; and Mr. Frank M. Woodruff, Chicago Academy of Sciences, for making the excellent photographs which illustrate this paper.

CHICAGO ACADEMY OF SCIENCES

[1] "The Probable Origin of Certain Birds." *Science*, n. s., vol. 22, p. 431, 1905.

NOTES ON THE GENUS LEPTOPHRYS

WILLIAM A. KEPNER

In the year 1869 Hertwig and Lesser published in the *Archiv für mikroskopische Anatomie* (Supplement zu Banden 1–8) an article entitled "Ueber Rhizopoden und denselben nahestehende Organismen." On page 57 of this volume they describe a new genus which they name Leptophrys. The following is their diagnostic description of this genus: "Body variable in form, sheet-like with processes put out, pointed and unbranched pseudopodia, which are chiefly found at the end of the processes; the parenchyma is filled with small non-contractile vacuoles nearly equal in size"; and though they saw but three bodies in a *single* individual which they took to be nuclei and failed to see nuclei in any other specimens, they add: "Nuclei in great number." The color or its absence in the "pearl-like" granules served them as a basis for distinguishing the two species, *L. cinerea* and *L. elegans*.

In December, 1904, I discovered in some water taken by Mr. William G. Lapham from an oozy bank near Afton, Virginia, a large Vampyrella-like specimen (Fig. 1), which except for the absence of nuclei and the variable size of the vacuoles answered in detail to *Leptophrys elegans*. In size the creature would cover a circular surface whose diameter was 80 micra. It was very active, constantly changing its form laterally, though dorso-ventrally it maintained a film- or sheet-like structure which was about 5 or 10 micra thick. The protoplasm was highly vacuolated by non-contractile vacuoles. The degree of vacuolation varied at different stages of vital activity. When most highly vacuolated the vacuoles approached equality in size. The body was also marked with numerous, more or less equal, "pearl-like" granules. The rather short, unequal, pointed, and unbranched pseudopodia were given off from the margin of the body. They contained no vacuoles nor refractive granules. When vacuoles and refractive granules were pushed out they formed processes which might bear one or more pseudopodia. Most of these were given off from an absolutely transparent marginal layer of protoplasm. Subsequently

FIG 1.—Scale : 1 mm. = 1 micron.

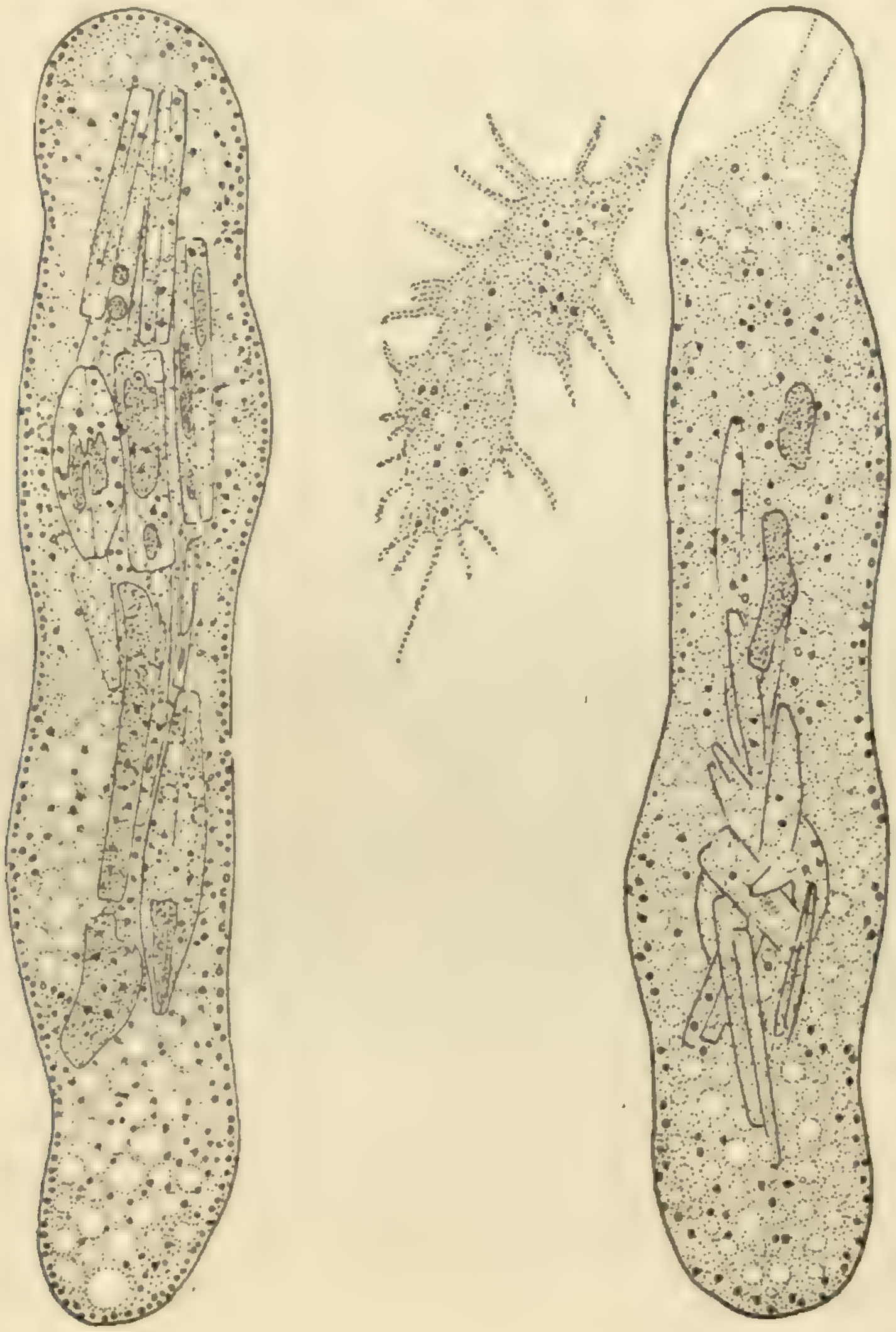
numerous specimens were found which did not show such a clear margin. Many specimens were seen which were quite free from food particles, but no staining of these would bring out a differentiation between the refractive granules and what might have been taken for nuclei. The figure of Hertwig and Lesser leads me to suspect that what they had taken for nuclei with central "nucleoli" were monads ingested as prey. It is unfortunate that they did not state how they determined these bodies to be nuclei.

Locomotion is effected by a more or less active amœboid movement. An active large individual tosses itself about very much as a cloud of smoke is distorted by a current of air. On the other hand the movement may be slow and deliberate.

The large individual represented in Fig. 1, took in as food diatoms, desmids, and what may have been several Infusoria. On March 22, 1905, in a bottle, that since March 12 had contained living *Chlamydomonas reticulata*, I found numerous specimens some of which belonged to *L. cinerea* and others which I had to place under the species *L. elegans*. They were feeding upon the Chlamydomonads. In one case I saw an individual that had ingested at least 25 Chlamydomonads. These flagellate forms after being ingested were greatly reduced in size. One specimen was found which had ingested a single *Navicula* sp. The ingestion of food was carefully observed. It was done, so far as could be seen, just as an Amœba envelops its food, but the closing of the ectosarc about the prey in the fashion of an iris diaphram could not be made out. The food appeared to be partially digested while the animals moved about. This inference is based upon the broken-down appearance of the ingesta. The food is eventually assembled into a common vacuole more or less centrally disposed.

Some time after the animal has gorged itself with food, or formed a central common vacuole of food, it withdraws its pseudopodia and enters into an encysted condition. Numerous cysts have been seen and studied. A single individual has been observed ingesting food and was followed through its complete encystment. From the time when the animal had quieted down and ceased to ingest food to when it left the cyst, a period of five hours had elapsed. The cyst varies in size and shape, depending upon the size of the

animal and the amount and form of the food. When the food vacuole contains rounded bodies like Chlamydomonads the cyst is spheroidal in form (Figs. 5 and 6). One animal was seen encysted about a single *Navicula* sp. In this case the cyst was oval (Fig. 4); in Fig. 2 is shown an encysted individual which had

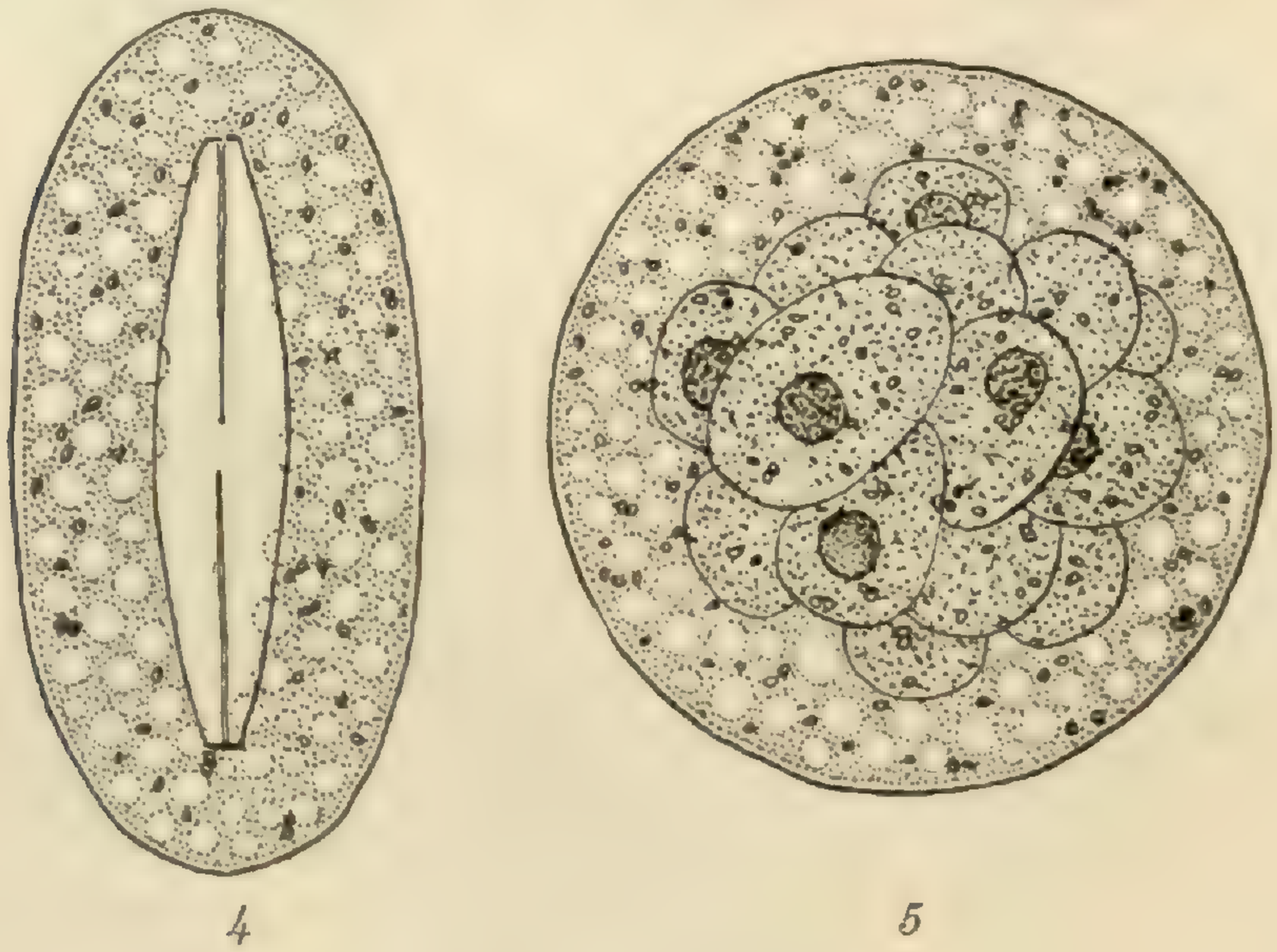


FIGS. 2 and 3.— Scale: 1 mm. = 1.18 micra.

a food vacuole of numerous long bodies that determined an elongated cyst. The animals vary greatly in size. Fig. 1 represents an individual that is somewhat larger than the average; the cysts of course are found to vary as greatly in size.

Upon encystment the animal is colorless or nearly so (Fig. 5). During encystment a color is assumed in some cases, which seems to depend upon the character of the food that is being digested.

In cases where Chlamydomonads were being digested and reduced in size the food lost its green color and gradually became dark brown (Figs. 5, 6). As this proceeded the refractive granules and the protoplasm took on a brownish tint, which was evidently due to products of assimilation (Figs. 6, 7). On the other hand in two observed cases where diatoms, desmids, and Infusoria were being digested, no coloration was noted (Figs. 2, 4). During the early part of the encystment the vacuoles are not conspicuous. As the end of the encysted condition approaches the vacuoles become more prominent. The cyst may rupture at one, two, three, or four places, and the contents escape through the clefts. In the



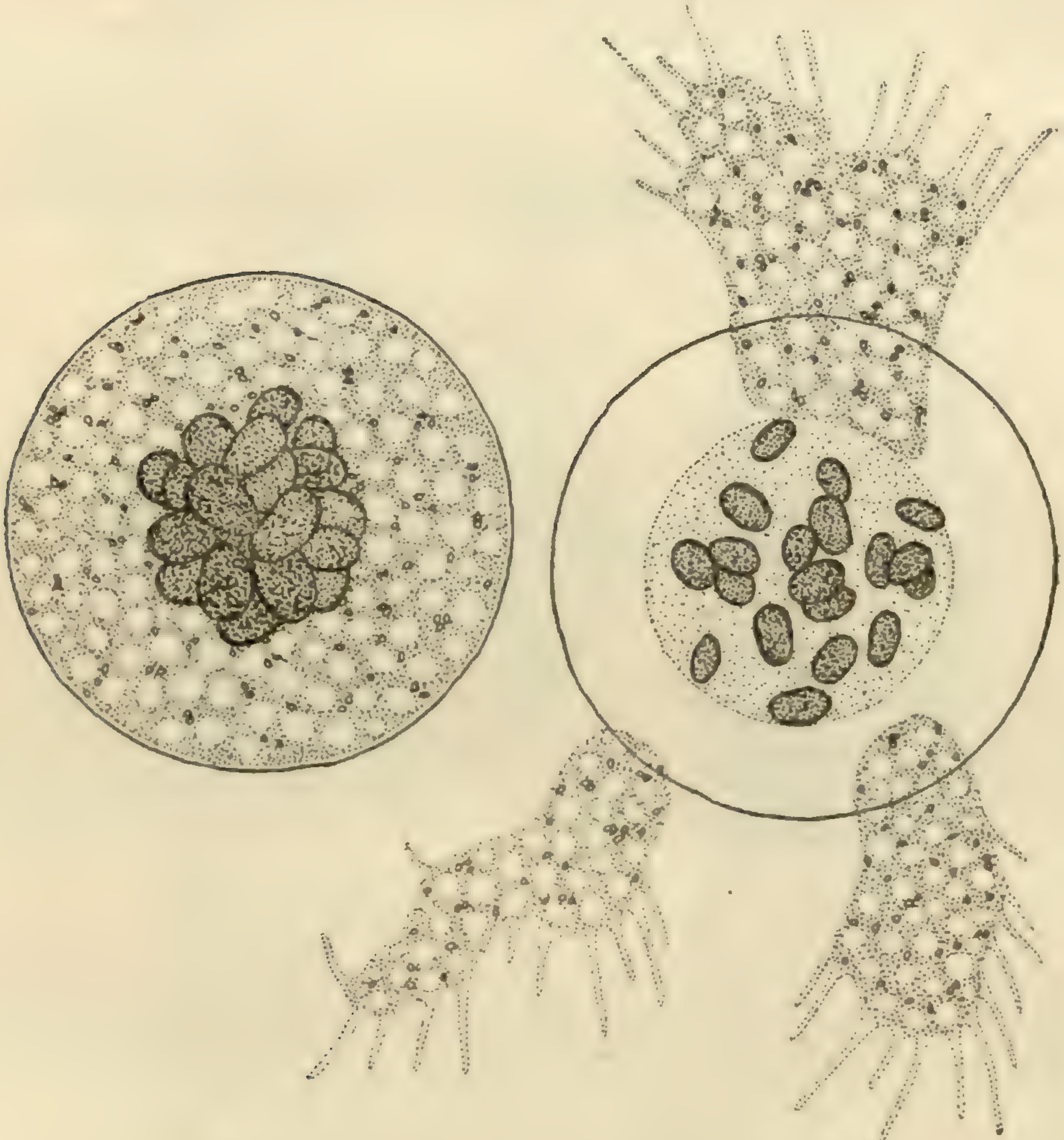
4 5

FIGS. 4 and 5.—Scale: 1 mm. = 1 micron.

large cyst shown in Fig. 3 the protoplasm streamed out at a cleft in the apparent upper right hand corner of the cyst. As the protoplasm flowed out it broke accidentally into four greatly unequal portions. Each part, though no two were equal in size, became a complete individual. These daughter individuals were almost colorless. In the forms that had been feeding upon Chlamydomonas the contents emerged at two, three, or four clefts in the cyst membrane (Fig. 7). In all these cases the daughter individuals came out of the cyst colored *light brown*. *As they lived an active life their color decreased.* Beneath a single cover-glass all degrees of coloration were easily found. The transparent ones answered to Hertwig and Lesser's description for *L. elegans*. The

brown ones as they leave the cyst, I take to be their *L. cinerea*. In as much as they had not seen any specimens ingest food and had observed no encystment I am led to believe that what they studied and described as two species were but different nutritive conditions of individuals of the same species.

In November, 1904, Mr. Lapham observed a large colorless



6 *7*

FIGS. 6 and 7.—Scale: 1 mm. = 1 micron.

individual divide into daughter parts of protoplasm to each of which the food enclosures had been equally distributed. In March, 1905, I observed one of the individuals found living with *Chlamydomonas reticulata* divide into daughter forms. The process was rather slow. It began with the formation of two fan-shaped parts, connected by a wide neck (Fig. 8). This neck became more and

more attenuated until at the end of 35 minutes there was the merest strand of protoplasm connecting the two parts, which had now moved 500 micra apart. This strand suddenly snapped and the fragments moved away as two new individuals. While this process was going on one of the parts ingested a Chlamydomonas. Except for this there was not a trace of ingesta within the dividing protoplasm.

These observations seem to afford reasons for setting aside Hertwig and Lesser's two species, *L. cinerea* and *L. elegans*; and the fact that, although there was ample opportunity to demonstrate nuclei such as Hertwig and Lesser describe as seen in part of a single individual, no evidence of their presence was obtained, leads to the conclusion already suggested by Penard that the genus Leptophrys is but a synonym for a species of Vampyrella.

The variation in the form of the cysts of this Vampyrella and the two cases of binary fission, independently observed by Mr. Lapham and myself in this species, are of interest. Attention is also called to the

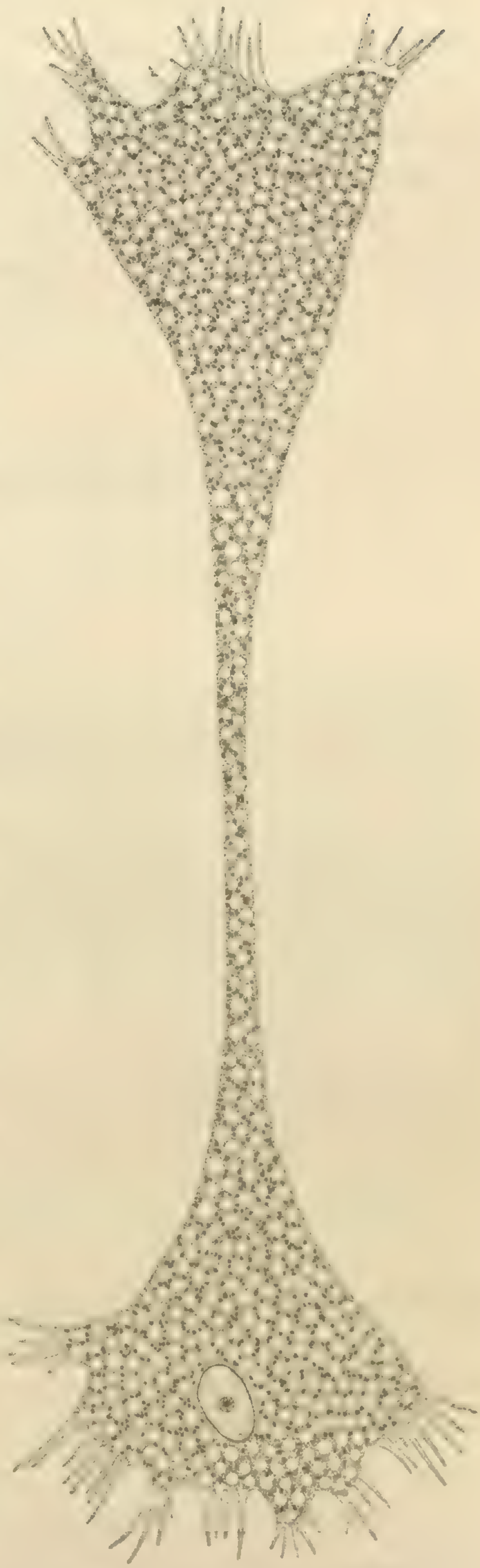


FIG. 8.—Scale: 1 mm. = 4 micra.

apparently accidental division of protoplasm that takes place where there is no centralized nucleus.

I am indebted to Mr. A. H. Tuttle, of this laboratory, for suggestions of value to me in preparing this article.

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EGG-LAYING OF CRAYFISH

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In crayfish, as in related Crustacea, the eggs are carried fastened to the limbs of the abdomen during the long period of development that precedes their hatching. As the openings of the oviducts are upon the thorax, the eggs have to be transported some distance to reach the abdominal limbs. It is the purpose of this article to describe some of the activities of the female associated with the extrusion of eggs from the oviducts, their transportation to the limbs of the abdomen, and their fixation there.

In a crayfish in France, a species of Astacus, some of the behavior of the female in laying was long since made out by Chantran (*Compt. Rend. Acad. Sci. Paris*, vol. 71, pp. 43–45, 1870; vol. 74, pp. 201–202, 1872) in his long continued and careful study of the life history of the crayfish. His too brief statements are as follows. The female crayfish stands up and for several hours secretes a viscid mucus from the limbs of the abdomen. It then lies down upon its back with the abdomen bent forward toward the openings of the oviducts, in such a way as to form a sort of chamber, in which, on the following night, the eggs were received as they were expelled from the reproductive organs. In different females the expulsion of eggs lasted from one to several hours. The eggs were plunged into the mucus which, as it were, bound the edges and the end of the abdomen to the thorax and also helped to make the boundary of the above mentioned chamber or basket. In this chamber there was some water as well as eggs and mucus. All the eggs were laid at one period and rarely were any laid in the day time.

Observations upon the laying habits of an American crayfish, *Cambarus affinis*, as published in this journal (*Amer. Nat.*, vol. 38, pp. 165–206, 1904) showed a close agreement with the above account. Renewed observations upon the same species in April, 1904, have added more details and verified suppositions previously made to bridge over gaps in observation of actual extrusion and transport of eggs.

The activities of the female connected with egg-laying may be divided, for convenience of description, into four periods. First, the preparatory cleansing of the under side of the abdomen and thorax. This lasts four or five days and has been described in the previous paper. Second, the period of secretion of mucus, or "glairing" as we may call it, to be described below. Third, the period of actual extrusion of eggs, previously inferred but described below as actually seen. Fourth, the rhythmic alternation of position of the body, or "turning," lasting several hours and described in the previous paper.

All these processes precede the long care of the eggs as they hang fastened to the abdominal legs for from five to eight weeks till they hatch, after which there is a brief period of association of female and young before the latter scatter and become independent.

The least well observed process is that of secreting glaire from the glands of the abdominal appendages and sterna. It always follows the long and very laborious cleansing of those surfaces and immediately precedes the extrusion of eggs so that as soon as the glaire is ready and the female properly posed, the eggs pass out into the glaire, one period passing insensibly into the other. At the time of secretion the female is still easily alarmed and moreover the glaire is at first seen with difficulty as it is like water in refraction, so that in most cases the "glairing" period escaped observation. But as far as was made out the secretion of the glaire took less than half an hour, though Chantran speaks of Astacus as secreting mucus for several hours. Possibly some of this time was taken up with "cleansing," which has not yet been noticed in Astacus. But if there is an actual time difference between Cambarus and Astacus it may be due to differences in temperature since Astacus lays in winter and this Cambarus in spring.

The details of the activities of a crayfish observed during the "glairing" process were in one case as follows. At first the animal kept the same unusual attitude assumed in cleansing itself, that is, it stood high up on its legs with the thorax and abdomen raised far above the bottom. The abdomen was bent forward loosely and its caudal fan reached nearly as far as the

middle of the abdomen. The small limbs of the abdomen, the pleopods, swung slowly back and forth with interruptions and then, after three minutes, flapped actively back and forth. Three minutes later the crayfish gave up this attitude and crouched down and turned slightly over to one side while still swinging the pleopods and also making very active fanning movements of the exopodites of the maxillipedes. After four minutes the crayfish again stood up and swung the pleopods back and forth for five minutes and then a faint halo of glaire was first detected about the pleopods. The abdomen had now become bent forward in a curve so that it resembled a half-closed hand and the space so enclosed seemed filled with an almost invisible glaire. When the pleopods inside this mass moved there resulted a jerky movement of dirty lines where the glaire and water met at the anterior opening of the chamber formed by the bent abdomen. Two minutes later the animal ceased to stand up and lay upon its left side with all the right legs high in the water, but after lying thus for two minutes it turned onto its ventral side and crouching prone, raised its third, fourth, and fifth legs on the left side, but coming against the side of the dish, did not roll over onto its right side as was expected. By this time the long continued and increasing contractions of the muscles of the abdomen had flexed it so far forward that the tail-fan reached to the bases of the second thoracic legs, leaving only the mouthparts and the bases of the chelæ and second legs exposed to view. The pleopods were still moving rapidly back and forth inside the glaire chamber. Two minutes later, some of the legs on the right side were raised and the animal seemed about to turn over onto the left side but it returned to the ventral position. The abdomen had now become flexed even more powerfully so that its terminal piece, the telson, reached to the bases of the chelæ, or first thoracic legs, and it was pressed upward against the thorax so that some of the slightly turbid glaire was forced out from between the tail-fan and the thorax. With the abdomen thus carried forward under the thorax, the animal remained six minutes crouching down so that anteriorly the ventral side of the thorax was near the bottom of the dish while posteriorly the *dorsal* side of the abdomen rested upon the bottom. Then all the right legs were raised and the body slowly

swung about through 120° till the right chela came against the end of the dish and the animal turned over onto the left side and rested with the anterior part elevated and the abdomen upon the bottom. Lying thus for some minutes the crayfish made no movements of any external organs. The tail-fan had receded a little but was still as far forward as the bases of the second thoracic legs.

Two minutes later, *i. e.*, about half an hour from the beginning of the "glairing" process, the continued recession of the abdomen laid bare the bases of the third legs and over the edge of the telson an egg was seen in the glaire above the telson. Thus the glairing period had already passed and the extrusion of eggs had been going on. A minute later the withdrawal of the abdomen stretched the glaire like a membrane from the edge of the telson to the region of the anterior thoracic legs and through this veil rows of eggs were seen issuing out from the opening of the oviduct on the base of the third right thoracic leg. The extrusion of eggs, however, will be described below from other more normal cases in which the crayfish lay upon its back and not upon one side when the eggs were extruded.

The actual extrusion of eggs was seen in six crayfish and took place in approximately the following number of minutes in these cases: 10, 10, 13, 17, 20, 30. This is in strong contrast to the statement of Chantran that, in Astacus, the extrusion of eggs lasted from one to several hours. Possibly he confounded the period of extrusion with the following period of "turning" which may well exist in Astacus and which in Cambarus occupies several hours.

In Cambarus as in Astacus it was very unusual for eggs to be laid in the day time and the above six cases were seen in the day time only from the employment of the following expedient. Crayfish that had finished the cleansing process were prevented from laying by being kept all night in running water barely sufficient to moisten them and then put into deeper water in the day time. After two or three repetitions of this treatment some ten females laid in the day time, several hours after being put into deep water.

Though no crayfish laid when merely moist, one small specimen

laid in water so shallow that the animal could not cover its back when crouching down as close to the bottom as possible. This female carried on some turning movements after laying and after forty-three days the eggs, apparently all of them, hatched out, contrary to expectation.

Some individuals, however, could not be forced to lay in the day time even by numerous repetitions of the alternating conditions. Such crayfish did not lay at all, yet when examined some were found to have the ovaries full of large eggs. Others kept for two months gradually resorbed the ovarian eggs. In such ovaries the old eggs were reduced to isolated, irregular yellow masses scattered throughout the ovary, while translucent new and minute eggs filled in much of the space between the degenerated eggs.

In the cases of egg-laying observed under the above forced conditions the extrusion of eggs followed after a thorough cleansing of the region that then secreted copious glaire. By the bending of the abdomen there was then formed a chamber, or basket, full of glaire, a sort of "incubatory pouch" which received the eggs and in which they were made fast to the pleopods. The way in which the tail-fan expands to close in this pouch and the part played by the glaire, or mucus, were well described for Astacus by Lereboullet in 1860 (*Ann. Sci. Nat.*, zoöl., ser. 4, vol. 14).

Being thus provided with a basket full of glaire the female after a few trials lies down upon her back, a most remarkable position considering the energy with which such crustaceans avoid it and escape from it at other times. The flexure of the abdomen becomes so excessive that the telson is brought up as far as the bases of the chelæ, or even to half cover them, and thus the glaire is smeared over all the ventral surface of the thorax near the oviduct openings upon the bases of the third, or middle, pair of legs. The eggs will thus come out into a bag of glaire and though laid under water they are not laid into the water. The gradual relaxation of the abdomen finally uncovers the bases of the third pair of legs so that the eggs may be seen coming out of the oviducts. This withdrawal of the abdomen does not, however, expose the eggs to the water since the viscid glaire that has been put upon the thorax is drawn out from the thorax to the

receding telson like an apron that covers over the eggs and prevents them from falling out even when the female turns right side up. This is the condition indicated in Fig. 5 of the preceding article in this journal.

While the eggs are emerging, the crayfish is almost motionless, lying supine with stiffly outstretched limbs and open claws as if dead. If now removed from the water and held in the hand the crayfish responds but little and the flowing out of eggs continues and may be more closely watched.

The mouths of the oviducts are widely open and remain fixed in that state when the crayfish is plunged into boiling water. It is then seen that the oval membrane that usually covers the opening is pulled outward like a curtain leaving a somewhat triangular orifice bounded on the external edge by this drawn curtain and on the median edge by the rounded rim against which the curtain comes when it is closed. Deep inside the large orifice opens the smaller oviduct tube full of eggs, each filling the tube from side to side. These eggs are also fixed by the heat in something of their natural irregular form. In life the eggs come out distorted by pressure and are so soft and flowing, like liquid in thin bags, that they mutually flatten against one another and become indented by contact with solid objects.

The eggs generally emerged in two streams one from each oviduct, but in some cases only one oviduct was used for a long time. The rate at which the eggs came out varied from 12 to 60 a minute on each side. With some stoppages and changes in speed some two to six hundred eggs were laid, by different females, in less than half an hour. Frequently the eggs came out in sets of three flattened together and the last one of the set rounded itself off during the brief pause before it was pushed away by the coming out of the next set. Thus the mouth of the oviduct was alternately taken up with one rounded egg and with three flattened eggs. When the end of deposition drew near, a gradual ending was brought about in one case by a cessation of all flow for two minutes and then the emergence of only two eggs, the last to be laid. When this animal was dissected an hour later the ovary was empty save for three eggs in the posterior lobe and two in the left oviduct and one of these slipped out of the mouth of the ovi-

duct when the ovary was being removed. Both oviducts were greatly distended, though for a long time only the right one had been discharging eggs.

The glaire into which the eggs come is dense along the edges of the abdomen and can be picked up by forceps as 'blobs' that hang down a half inch or so, supporting their weight. But the rest of the glaire is too weak and watery to be pulled away. When the abdomen was forcibly bent back to examine this glaire and the female prevented from laying for a night there was no second secretion of glaire over laying though cleansing movements were carried on again. When the crayfish laying eggs was suddenly put into boiling water the glaire coagulated sufficiently to form an opaque white mass over the eggs in the posterior part of the abdominal basket but the glaire over the issuing eggs did not become opaque enough to hide their red color.

The transfer of the eggs from the oviducts to the pleopods within the abdominal chamber is purely the work of gravitation. Though the crayfish lies upon its back the abdomen is always lower than the thorax and in some cases several legs were actively braced against the bottom of the dish in a manner to exaggerate this sloping of the body. In one case the animal sat propped up at an angle of nearly forty-five degrees supported upon its short fifth legs and upon the abdomen. Generally, however, only the tip of one chela and one leg touched the bottom and thus gave more stability to the animal as it lay upon its rounded back.

The deep groove between the bases of the thoracic legs favors the backward flow of the eggs which coming from each oviduct unite in one stream that flows along the thorax onto the abdomen and there divides to flow right and left along the bases of the pleopods. When, as is often the case, the animal lies with one side higher up than the other the eggs coming out of the more elevated oviduct drop some 6 to 8 mm. diagonally across the body before reaching the sternal surface. In such positions also the eggs accumulate in the lower side of the abdomen and when the animal is taken in the hand the eggs will flow right and left in the abdominal chamber as right or left is held lower. The glaire is thus not dense enough to stop the movement of eggs except at the edges of the chamber and upon the pleopods. Even after

the period of extrusion and six minutes after "turning" had begun, when an undisturbed female was taken out of the water many of the eggs in the chamber ran over from side to side and tended to escape at the angle between the abdomen and the thorax on each side. Some of the eggs were then loosely attached to the pleopods, but when the abdomen was forcibly straightened out and held downward many of the eggs glided off over the end of the telson.

Though the details of action of the female at the time of extrusion of eggs were different in other cases the following special case is thought to be, in the main, typical. A crayfish lying upon its back with the telson so far forward over the thorax as to reach to the posterior edges of the second legs showed no movements of any organs for a minute and then only a slight motion of the antennules and of some legs. After four minutes more there were some slight movements of the third legs and of the left chela. The right chela rested upon the bottom of the dish and so held the animal in more stable equilibrium. By this time the slow relaxation of the abdomen had let the telson glide so far back that the bases of the third legs were nearly uncovered. Three minutes later by looking in under the telson one could see eggs coming out of the openings of both the right and the left oviducts, which openings are upon the bases of those legs.

Where the tail-fan had been over the thorax, as far forward as the chelæ, there was left a layer of glaire. On counting the eggs in the issuing streams, still three minutes later, they seemed to come out at the rate of one a second on each side. The only movements of the animal were a temporary fanning motion of an exopodite near the mouth. But five minutes later the animal had turned to lie with the left side somewhat elevated and the eggs were seen falling out of the oviduct of that side across the body then to glide back into the abdominal basket. A minute later they were coming out at the rate of ten in sixty-five seconds, in groups of two or three at one jet and then an interval before the next row of two or so. In another minute there were signs of life in the rapid fanning of exopodites on the left of the mouth, which continued for a minute, nearly stopped, and then started again. After a minute more there were added a rolling of the

entire body onto an even keel and then a violent struggling of the legs as if to turn the body over into the normal prone position. Eggs were still seen in the mouths of the oviducts, two on each side. In this struggle to regain the ventral position the left side was down for a minute and then the right for a minute when the right going under and the left uppermost the animal got onto its ventral side. It then stood thus, on its legs with ventral side down, for two minutes with only slight movements of two or three legs. Immediately after this brief rest the "turning" movements began. This would no doubt have gone on for several hours but it was checked by interference after six minutes during which time there were fairly regular alternations of pose, this animal lying down first upon its left side and next upon its right.

It is in these turning movements that always follow the extrusion of eggs, that the eggs become fastened to the pleopods, so that when the female a few hours after the eggs have come out, for the first time straightens out the abdomen and the glaire is seen only as shreds hanging from the edges of the abdominal terga and from the tail-fan, the eggs do not fall into the water but henceforth hang suspended from the pleopods, till hatched.

While fastened to the pleopods the developing eggs are protected by the female and also aërated by special movements of the pleopods which are the more energetic the more the water tends to be stagnant or poor in oxygen. In all probability eggs not attached to the pleopods would never develop, in nature, and this attachment seems an essential part of the life history, here, as in many other Crustacea.

Just how the fastening of the eggs takes place is by no means clear. A microscopic examination of the so called "cement glands" upon the sterna and all the six pairs of appendages of the abdomen showed that in Cambarus, just as in Astacus, these glands contain the material from which the "glaire" is made. The same reasons that led Lereboullet (*l. c.*) and later Braun (*Arb. zoöl.-zoöt. Inst. Würzburg*, vol. 2, 1875) to believe that in Astacus this secretion fastened the eggs to the pleopods, apply in Cambarus and there is little doubt that this glaire plays the most important part in fastening the eggs. However, the remarkable fact that in both these crayfish as in crabs the eggs are fastened

almost exclusively to *hairs* upon the pleopods and upon the sterna calls for explanation. In crabs Williamson (*22d Ann. Rep. Fisheries Board for Scotland*, 1904) has recently described special hairs upon the pleopods as piercing the outer egg-case and liberating an adhesive substance contained between the inner and outer part of the egg-case. His idea is that the eggs are first impaled in a row upon a hair, as upon a skewer, and subsequently fastened to the hair by the collapsing of the pierced outer egg-case and by the adhesive material contained within it. As Williamson sought to extend this view to the lobster and other Macrura, the crayfish, Cambarus, was reëxamined in April, 1905, to see if this view would apply here, but no evidence of such skewer action of hairs was found though on the other hand no *absolute* refutation of such a view was obtained.

In *Cambarus affinis* preserved eggs have in the ovary a case about $\frac{1}{3}$ μ in thickness as seen in optical section. When they leave the enveloping cellular follicle and are laid and for at least five hours afterwards, they have the same thickness of case but twenty-three hours after laying the case was (observed as above) 2 μ thick. In live eggs there is a remarkable change in elasticity accompanying this change in thickness of case. While the fresh-laid egg glides along like a liquid drop flattened and deformed by every contact and scarcely held together by its delicate case, the egg thirty-six hours afterwards is a tensely spherical ball, which, dropped nine inches onto a table, rebounds five inches and continues to bounce up and down five or six times before coming to rest. This great elasticity was noticed in Astacus eggs also, by Lereboullet. Such eggs, however, are normally hung to the pleopod by peculiar stalks. Each egg has its separate stalk and this is of elastic material comparable to the egg-case.[1] When this stalk was pulled out to four or five times its length, to ten times the diameter of the egg, it flew back like a rubber band, as soon as released.

These stalks are not formed until a little while, 15 minutes or so, after the eggs enter the abdominal chamber and at first they are

[1] In a few cases an egg had two stalks with a ribbon-like connection over the surface of the egg.

exceedingly delicate, soft, wide, flat bands. These are at first very short and only slowly become as long as the diameter of the egg, subsequently to become many times that and hard and narrow and twisted. In this latter state they remain after the egg hatches and connect the empty egg-case with the pleopod and are even then a means of salvation for the young.

Near the egg the stalk expands as a rounded tent, or bell-like membrane the edges of which are fast to the egg-case over a rounded area about one third the diameter of the egg. Optical sections indicate that the stalk continues by this membrane over the egg to make its thick elastic outer case while the thin inner case is the only one near the egg over the area covered by the bell. At this place only there seems to be a liquid separating the inner case from the walls of the bell. The stalk seems hollow for some distance up from the bell and one is led to infer that each egg is slung in a bag the closed mouth of which, when drawn out, forms the stalk. The stalk and bell look like glass, but have longitudinal creases that simulate a fibrillation. The other end of the stalk is continuous with a flat mass that binds together many of the plumose hairs along the side of the pleopod. In fact, these hairs seem rather completely invested in a secretion which holds them all imbedded in a flat mass on each side of the pleopod while from the edges of this mass hang out the egg stalks at intervals, every five or six hairs having their investment continued out as a free stalk for an egg. The stalks are like a fringe from a curtain in which the hairs are fixed; but many stalks arise from the flat sides of the curtain.

The structure of the stalk when magnified four hundred diameters is homogeneous on the outer surface but within is a clear matrix full of vesicles about $1\frac{1}{4}$ μ in diameter and elongated in the length of the stalk as if by the stretching of the matrix. When broken, in its early stages, the jagged edges of the stalk round off slightly as if somewhat paste-like.

Some facts that seem to increase the difficulty of applying Williamson's view to Cambarus are the following. One female was found in which the sterna and pleopods of the first somite were not clean and these alone had no eggs attached to their hairs so that the painfully laborious process of cleansing seems necessary

for attachment of eggs, and this is more readily reconcilable with the idea that a secretion flows out over the cleansed surface to fasten the eggs than with the idea that the hairs puncture the egg-case and so liberate the material for fixation.

The "perivitelline space" which is held by Williamson to contain the adhesive material in crab's eggs seems to exist in Cambarus as the result of strong, abnormal osmotic changes only, which may accumulate liquid between the inner and the outer parts of the egg-case, when for instance an egg is plunged into strong Flemming's liquid this may accumulate in local blisters of the outer membrane.

Ovarian eggs were not sticky unless allowed to dry upon the surface when they, *either with or without the enclosing cellular follicle*, stuck to a needle and might be pulled up into club-shaped drops that then sprung up to hang as bulbs connected to the needle by a minute stalk.

The glaire, however, sticks slightly to dishes and to a knife and when eggs were taken out of the glaire from the front part of the abdominal chamber where they had not yet made stalks (though others in the back part had done so) and put into a watch glass of glaire, they stuck together more firmly than when left in water. The connection of these eggs with one another after 48 hours was by delicate fibers something like early stages of egg stalks and such eggs after fifty-eight hours were elastic so that they rebounded five or six inches when dropped nine. Thus in glaire the elastic case and something like a stalk were made when isolated from pleopods and hairs. Again, eggs broken off from very young stalks and left in moist air adhered together very firmly and also to a dead pleopod. These facts seem more readily explained by the action of the glaire than by an assumed early pricking of the hairs.

A microscopic examination of the material that binds the plumose hairs together, made some hours after the eggs were laid, showed that in some places this mass was a dense, clear, highly refracting sheet, moving and breaking under pressure like a stiff jelly, and identical with the stalks of eggs, while in other places the material on the hairs was a milky gray matrix that rounded itself off like a viscid fluid when broken and was full of droplets

like those inside the cement glands. It may be that the secreted glaire passes from the latter state into the former.

The glaire itself resembles the stalks in being a clear matrix full of droplets that elongate when the glaire is stretched but while some of the droplets are $1\frac{1}{4} \times 12\frac{1}{2}$ μ others are as large as $37\frac{1}{2} \times 112$ μ and many are compound emulsive drops of 12 to 25 μ. Glaire and egg-stalk are thus not identical though the stalk might well arise from glaire matrix.

Without, then, imagining any special action of the hairs we may suppose that the eggs become fastened to them because they are smeared with the densest secreted matter from the pleopod glands. All the surfaces having been made scrupulously clean the secretion can spread over the hairs as they hang like feathers in the water and as the glands along the pleopod are segmentally or interruptedly arranged, the hairs may well be stuck together in small clusters or brushes of denser glaire separated by more watery glaire. When the eggs roll down along these brushes smeared with adhesive glaire they may stick to them as the brushes stick to one another all along the side of the pleopod. Once stuck and more or less buried in the glaire on the hairs the pull of their weight will drag out enough glaire to make a stalk. That more eggs stick to the hairs than to the body of the pleopod may be largely a matter of relative area.

Some eggs that were loose in the abdominal chamber when the rest had stalks, some hours after being laid, presented the following peculiar appearance upon one side. A rounded area agreeing with the size of the bell of a stalk was thickly set with minute drops on the outside of the outer egg-case while fine threads inside this case suggested that some filose, or else secretional activity of the egg might have been going on over this area through pores in the egg-case. As was known to Chantran, each egg has a large polar area and it seems possible that special activities of the protoplasm there may be concerned in localizing the attachment of the egg to the glaire on the hairs and aid in determining the bell-like area of the stalk.

SUMMARY

The egg-laying habits of *Cambarus affinis* are closely similar to those of Astacus, as far as the latter have been described.

In Cambarus there are four periods of activity: cleansing, glairing, extrusion, turning.

The transportation of the eggs from the oviducts to the abdominal appendages is accomplished by gravity when the female places herself in special positions.

The activities of the female include a prolonged use of special tools to cleanse the surfaces later covered by the secretions of the "cement glands," a long continued maximum contraction of the abdomen, a habit of lying supine and externally inert during oviposition, and a long rhythmic alternation of poses associated with the fastening of the eggs to the abdominal appendages. After this follow the weeks of aëration and care of the eggs till they hatch.

While the ultimate analysis of the factors concerned in fastening the eggs to the abdominal hairs awaits future investigations the secretion of the "cement glands" seems of chief importance though local activities of the egg may possibly play a part.

BALTIMORE, MD.

SOWERBY'S WHALE ON THE AMERICAN COAST

GLOVER M. ALLEN

A CENTURY has now elapsed since Sowerby's whale (*Mesoplodon bidens*) was first made known to science by James Sowerby ('04) in his *British Miscellany*. During this period barely more than two dozen additional specimens have been recorded and these have more often been to a greater or less extent imperfect. Flower ('72) in his account of the genus, listed but ten specimens of this species known by him to be at that time preserved in the museums of the world. Seven of these ten specimens were represented by skulls only, while of the three others more or less of the skeleton was saved. Turner ('89) gave the number of known records for the occurrence of this whale as nineteen, and a few more specimens have since been made known, so that the general characters of the species are now fairly well ascertained.

At the time of Turner's writing (1889) but two examples of Mesoplodon had been recorded from the western side of the North Atlantic. The first of these was stranded on Nantucket Island, Massachusetts, in 1867 (Agassiz, '68), and its length is recorded as 16 feet, 3 inches (J. A. Allen, '69, p. 205). The second American specimen was captured on March 28, 1889, at Atlantic City, New Jersey, and was secured by Dr. F. W. True for the United States National Museum (Turner, '89, p. 13). Nothing further was known of the species in American waters until 1898, when a young female was found dead on the coast at Annisquam, Massachusetts, in August. Its skeleton was obtained by the late Professor Alpheus Hyatt for the museum of the Boston Society of Natural History. Save for a brief mention (Hyatt, '99) this specimen has not been reported upon.

I am indebted to Mr. Thomas Barbour, of New York City, for the privilege of recording a fourth American specimen and the twenty-sixth hitherto known. Mr. Barbour has very kindly written out the following notes respecting this interesting capture.

"On the 22d of July, 1905, a large specimen of *Mesoplodon*

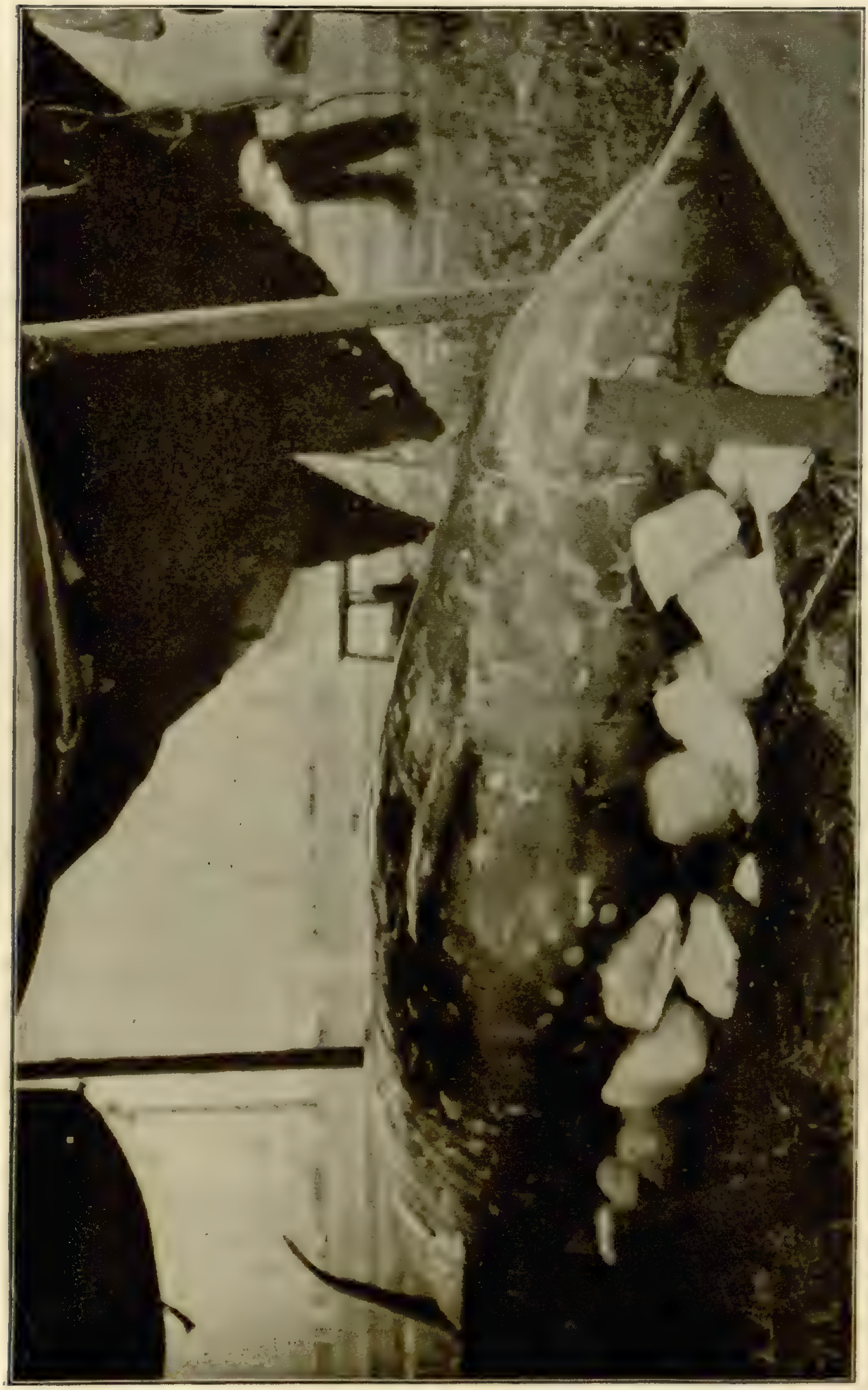

FIG. 1.—*Mesoplodon bidens*; North Long Branch, New Jersey. Ventral view. From photograph loaned by Mr. Thomas Barbour.

bidens became entangled in the pound-nets about a mile offshore from North Long Branch, New Jersey. It was rather exhausted when found, and was towed with some difficulty by two large power pound-boats to the beach, where it was secured by a rope. It soon died owing to injuries received during its capture.

"The total length of the specimen was said by the fishermen who measured it, to have been 22 feet. The coloration was very peculiar. The entire upper surfaces were slaty blue-black, the lower surfaces somewhat lighter. The sides and belly were dotted with numerous white spots, each varying from one to three or four inches in diameter. On the throat these patches became more or less confluent and very irregular in outline."

With some difficulty, Mr. Barbour succeeded in having photographs of this animal taken, two of which are here reproduced. The first of these (Fig. 1) shows the whale lying on its left side with the ventral portion toward the observer. The spindle-shaped form of the body, the small pectoral limb, and the beak-like snout are fairly well seen. As the anterior part of the animal's body was shaded by a canvas awning, the light spots and irregular throat-markings are distinctly seen in the photograph without the addition of light areas due to reflection, such as sometimes appear in photographs of parts taken in direct sunlight. The two diverging gular sulci are very well shown at the right-hand end of the figure, and are clearly not confluent at their anterior inception. One of these sulci (the lower in the figure) seems to be open, as though stretched apart by the dragging of the left side of the head. Fig. 2 is a view of the top and right-hand side of the head. The single crescentic blowhole with its extremities directed forward, is seen at *a*; what appears to be the right eye is seen at *b*. The very small mandibular tooth (*c*) is seen barely projecting from the gums and its small size indicates that the animal was probably a female. The lower jaw is clearly longer and broader than the upper, and a slight groove or gutter can be made out at the corner of the mouth.

The skull of this specimen was secured at considerable trouble by Mr. Barbour, and presented by him to the Museum of Comparative Zoölogy where it is catalogued as no. 7301. The mandibles and the rostral portion, however, were subsequently destroyed by an unfortunate accident.

It will be of interest to bring together a few notes on the Annisquam and the Long Branch specimens for comparison with other recorded observations on this species.

A considerable variation in the color seems apparent from the accounts of various authors, especially in respect to that of the

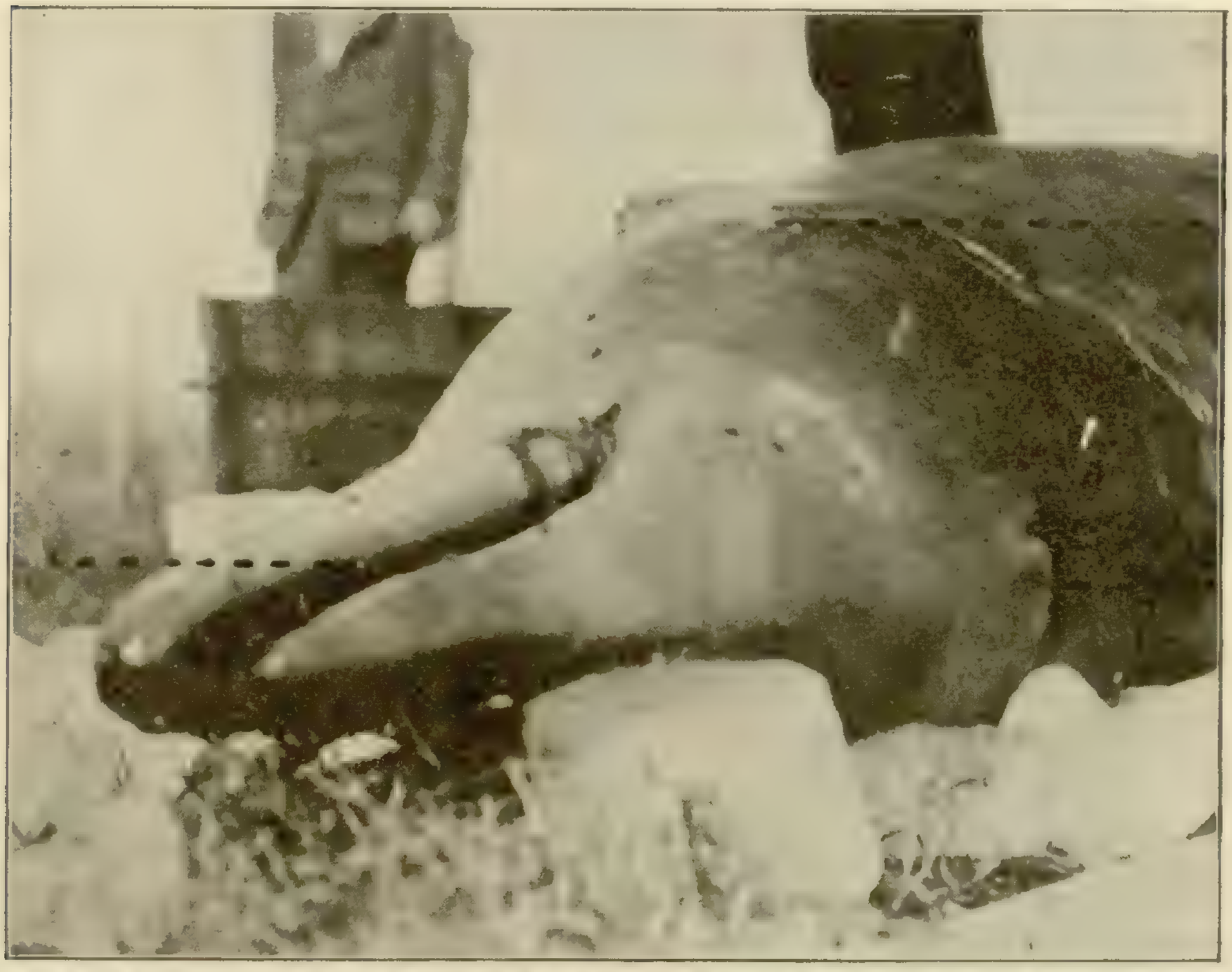

FIG. 2.— *Mesoplodon bidens*; North Long Branch, New Jersey. Top of head. *a*, blowhole; *b*, right eye; *c*, tooth. From photograph loaned by Mr. Thomas Barbour.

under parts. Turner ('89) summarizes briefly the descriptions given up to that time and concludes that there "can be no doubt ....that this animal is not of the deep black colour on the dorsum which one sees in Hyperoodon, but that the dark hue is dashed with a bluish tint, so that one may describe the prevailing colour of the back as dark bluish-gray or bluish-slate colour. The grey or whitish, almost circular spots....are obviously also characteristic markings of the skin. The belly is not white but of various shades of grey, dashed perhaps with a bluish tint." Southwell and Harmer ('93), however, describe the female stranded at Norfolk, England, Dec. 18, 1892, as of a uniform black color, "not appreciably lighter on the belly than on the back," with a "perceptible bluish tint on the skin in a good light." They note also

the light streaks and blotches "most numerous on the side and ventral surface." The large fetus contained in this specimen was a male and had the under parts "white." W. Rothschild ('93) accordingly suggests that it may prove in this species that the males have the belly white, while the females have this region of much the same color as the back and sides, save for the light blotches already mentioned. The Long Branch female seems to be of this latter type of coloration. Grieg ('98) found that the male taken at Karmö was colored much as Rothschild describes, with the back a blue-gray becoming lighter on the belly, which was nowhere *pure* white but tinged with reddish. The clear color of the belly extended from the gular folds to the genital opening, and there were none of the roundish circular spots to be discovered. Evidently the coloration was much like that of the Havre specimen figured by Dumortier ('39). Most of the recorded specimens, however, have not been examined while in a fresh condition by a trained naturalist and the few descriptions of the external coloration are insufficient to settle the question of a sexual dimorphism in this respect.

Regarding the Annisquam specimen, no color notes were taken, but from a few small photographs in the possession of the Boston Society of Natural History, it appears evident that the ventral portion was of a lighter tint, and in one of the views a few oval whitish spots are seen on the side a trifle behind the middle portion of the body. Another view shows the convexity of the posterior margin of the flukes at the median point as well as the prominent dorsal fin. The lower jaw protruded slightly beyond the upper. Measurements of this specimen, as noted by Professor Hyatt, are as follows: total length, 12 feet, 2 inches; from anus to bight of flukes, 3 feet, 4 to 6 inches; across the flukes, 3 feet, 1 inch; from tip of rostrum to angle of mouth, 1 foot, $1\frac{1}{2}$ inches. The gular furrows were noted as about 10 inches long and from $\frac{1}{4}$ to $\frac{1}{2}$ an inch deep.

The bones of the Annisquam specimen were macerated and cleaned, and are now preserved in the collection of the Boston Society of Natural History. The skeleton presents several points of considerable interest and through the kindness of Mr. Charles W. Johnson, the curator of the Society's museum, I have been enabled to make the following notes.

The skull shows the specimen to have been rather immature as

the sutures are largely unclosed; moreover, the rostral cartilage had not ossified so that the thin overarching premaxillæ of the rostrum form a long tube nearly closed dorsally except for a slight space where these bones do not quite meet along the median line. The proximal portions of the premaxillæ just anterior to a line passing across the middle of the blowhole, are nearly flat; they then rise almost perpendicularly to the vertex of the skull and seem to overhang the blowholes but slightly, although this relation is somewhat obscured owing to a slight injury. The maxillary bones *slope downward* from their junction with the premaxillæ to the rim of the cranium. In the Long Branch cranium, which is that of an animal fully adult, the broad proximal portions of the premaxillæ are slightly hollowed in front of the nares, and rising to the summit of the skull, overhang the blowhole by their greatly thickened antero-dorsal edges. In front and at the sides of the nares the maxillaries *are elevated* as much as 2.5 cm. above the adjacent premaxillaries, so that True's ('85, p. 586) statement in regard to Ziphius and Hyperoödon holds good also in some degree for Mesoplodon, namely, that "there appears to be a progressive excavation or absorption of the bones lying in the median line of the upper surface of the beak, accompanied by introvertion of the premaxillæ and a rounding off of the extremity of the beak."

In both the Annisquam and the Long Branch skulls the right premaxillary is slightly larger than the left and the right nasal opening is more convex in its exterior outline than the left. In both specimens the maxillary and the premaxillary foramina are on practically the same line with relation to the transverse axis of the skull, though in the Long Branch specimen the former is about 1 cm. behind the latter. In the Annisquam specimen the maxillary foramen is very large and its opening is below the level of the surrounding parts. It is continued forward as a deep groove or canal to the base of the rostrum, which is a feature practically lacking in the skull from Long Branch. In each ramus of the lower jaw there is a single tooth situated 25 cm. from the tip, or 3 cm. anterior to the middle point. From measurements given by Grieg ('98) for the two Karmö specimens the large tooth was situated at one third the jaw length from the tip in each. In the Cap Breton specimen, according to Fischer ('92) the tooth was three

sevenths of the jaw length from the tip, just back of the symphysis. The teeth of the Annisquam specimen barely projected above the alveoli of the jaws and are sharply mucronate. The basal portion of each, however, is more like that of the male's tooth in the slightly convex posterior outline and the forward extension of the anterior angle. Fig. 3 represents a lateral view of the tooth from the right mandible of the Annisquam whale; its extreme length from the point to the anterior tip is 55 cm.

The Annisquam skeleton has 45 vertebræ. Four of the seven cervicals are fused. The atlas, axis, and third cervical are firmly ankylosed throughout, save for the lateral foramina for the passage of the cervical nerves. The fourth cervical is fused to the third by the dorsal spine on the left side and by the tip of the upper lateral process of the same side. Its centrum, right half of the dorsal spine (the spine is divided medially), and the remaining lateral processes are free. This is the only case thus far recorded in which four cervicals have been found fused in this species for Reche's (:05 p. 171) statement that Flower has recorded a specimen the dorsal spine of whose fourth cervical was fused to the third, is a *lapsus*. Flower is here referring to *Ziphius cavirostris*. Grieg ('98) found that the first five cervicals were united in one of the Karmö specimens but the first two only in the other example and the same author (:04) found the first three fused in the Rugsund specimen (1901). Fischer ('92) records that in the Cap Breton whale the first two were entirely ankylosed while the centrum but not the spine of the third was fused with the second cervical. Aurivillius ('86) accredits the Bohuslän (1885) specimen with three fused cervicals. Turner ('85) found the first two only fused in the two Shetland examples and the same was true of these bones in the Skager Rack and the Vanholmen specimens (A. W. Malm, '71; A. H. Malm, '85). Van Beneden and Gervais in their *Ostéographie des Cétacés* give the number of

FIG. 3.— Lateral view of mandibular tooth of *Mesoplodon bidens*, female, Annisquam specimen. Natural size.

fused cervicals as three while both Van Beneden ('64) and Dumortier ('39) agree in stating that the first two only were fused in the Ostend 1835 example. The fusion of the first two is thus apparently the more usual condition. In the Annisquam whale the epiphyses of the fourth and fifth cervical vertebræ and the anterior epiphysis of the sixth cervical are fused to their respective centra, but all the other epiphyses of the vertebral column and of the pectoral limbs are free.

The Annisquam skeleton has nine dorsal vertebræ with their corresponding pairs of ribs, a number which agrees with that of at least four recorded skeletons though ten pairs of ribs are recorded in case of five others (Rugsund, 1901; Karmö, 1895; Shetland, 1885; Skager Rack, 1869; Ostend, 1835).

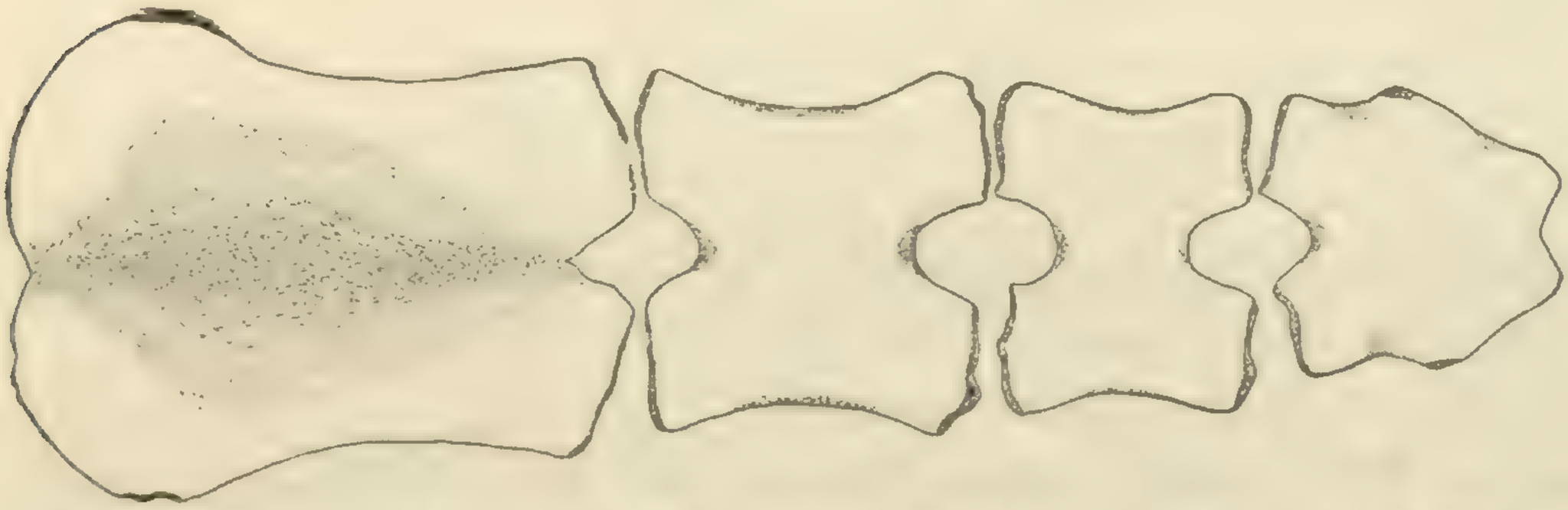

FIG. 4.—Sternum of *Mesoplodon bidens*, female, from above; Annisquam specimen.

The sternum of this specimen presents a few points of interest. It consists of four pieces, the anteriormost of which is largest, slightly hollowed above, and correspondingly convex below. The three remaining pieces are nearly flat, with a deep median notch at the anterior and posterior border of each. The most posterior piece evidently represents a fusion of the elements of two segments as there are articular surfaces for two pairs of ribs. Both the Karmö specimens (Grieg, '98) had sterna of four pieces and in each the fourth or most posterior piece seems to show articulating surfaces for two pairs of ribs. Apparently in these the very small sternal elements of each side corresponding to the fifth pair of ribs fused with the next anterior sternal segment but did not fuse medially with each other, so that a deep notch is left in the posterior margin of the last sternal piece. In the male Karmö specimen the notch is nearly closed posteriorly indicating a medial approxi-

mation of the elements of right and left sides, and thus approaches the condition described by Fischer ('92) for the Cap Breton specimen whose sternum was likewise of four pieces. The fourth was notched in front and had a central hole and a posterior notch. This central hole evidently corresponds to the two notches that would have been formed between the fourth and fifth sternal elements had they failed to fuse with each other. In the Annisquam specimen this space has been quite obliterated. According to A. W. Malm ('85) the sternum of the Skager Rack whale consisted of five pieces of which the two posterior were ankylosed, while that of the Vanholmen specimen was of four segments. Aurivillius ('86) states that the sternum of the Bohuslän skeleton was of four pieces of which the last is practically like the others save that the posterior notch is nearly closed. The sternum of the Rugsund specimen as figured by Grieg (:04, p. 33) is likewise of four segments, but the two elements of the fourth segment have not united medially while that of the left side is ossified with the next anterior piece. The 1885 Shetland whale had five sternal pieces (Turner, '85) but the 1881 Shetland example had four sternal pieces only, the posteriormost of which, as in the Annisquam skeleton, represented a fusion of the fourth and fifth pairs of elements (Turner, '82). Still another variation is seen in the Ostend specimen in which the two elements composing the fifth or posteriormost piece are separate both from the piece next anterior and from each other, while that of the left side is apparently displaced so as to be in advance of the corresponding element of the right side (Van Beneden, '64, pl. 3, fig. 2). An additional point of interest in the Annisquam sternum is its bilateral asymmetry for the right-hand element of each of the four pieces is slightly longer than that of the left side (Fig. 4). Thus the extreme lengths of the right-hand elements in centimeters are: 15.1; 8.4; 6.0, and 7.1, while those of the left-hand elements are 14.7, 7.9, 5.85, and 6.8 respectively. A like asymmetry is seen in Grieg's figure of the Rugsund specimen.

For convenience of reference, the known recorded specimens of Sowerby's whale are listed in the following table: —

Recorded Specimens of Mesoplodon bidens

No.	Sex	Locality	Date	Reference
1	male	Elginshire, Scotland	1800	Sowerby, '04
2	female	Havre, France	Sept. 9, 1825	Blainville, '25
3	male	Sallenelles, France	Summer, 1825	Deslongchamps, '66
4	female	Ostend, France	Aug. 21, 1835	Dumortier, '39
5	male	Brandon Bay, Ireland	Mar. 9, 1864	Andrews, '69
6[1]	male	Norway	before 1866	Van Beneden, '66
7	—	Nantucket, Mass.	1867	Agassiz, '68
8	male	Skager Rack	June 15, 1869	A. W. Malm, '71
9	male	Brandon Bay, Ireland	May 31, 1870	Andrews, '70
10	female	?Scotland	1872	Turner, '72; Flower, '72
11	female	Hevringholm Strand, Denmark	Feb. 3, 1880	Reinhardt, '80–'81
12	male	Shetland	Apr., 1881	Turner, '82
13	male	Vanholmen, Sweden	Oct. 30, 1881	A. H. Malm, '81, '85
14	male	Shetland	May 23, 1885	Turner, '85
15	male	Bohuslän, Sweden	Aug. 6, 1885	Aurivillius, '86
16	male	Yorkshire, England	Sept. 11, 1885	Southwell and Clarke, '86
17	male	Firth of Forth, Scotland	Oct., 1888	Turner, '89
18[2]	—	——	before 1888	Van Beneden, '88
19[3]	female	Norfolk, England	Dec. 18, 1892	Southwell and Harmer, '93
20	male	Cap Breton, France	Aug., 1888	Fischer, '92
21	female	Atlantic City, N. J.	Mar. 28, 1889	Turner, '89
22	female	Karmö, Norway	Aug. 25, 1895	Grieg, '98
23	male	Karmö, Norway	Aug. 29, 1895	Grieg, '98
24	female	Annisquam, Mass.	Aug., 1898	Hyatt, '99
25	male	Rugsund, Norway	Nov. 14, 1901	Grieg, :04, :05
26	female	North Long Branch, N. J.	July 22, 1905	

To this list should probably be added the record of a specimen found floating in the sea at the entrance of the British Channel about 1840. The skull of this whale is said to be in the museum at Caen (Flower, '78) and on it Gervais in 1850 founded his *Mesoplodon europæus*. Some confusion has also existed in regard to

[1]An incomplete lower jaw in the Museum at Christiania.
[2]An incomplete cranium without data in St. Petersburg Museum.
[3]Contained a large fetus.

the dates of certain of the captures. Thus Reinhardt ('80–'81) and Van Beneden ('88) have included examples of Hyperoödon in their lists of records; Gray ('66, p. 352) mentions a specimen from Havre, Aug. 22, 1828, and Van Beneden ('88, p. 98) apparently has quoted Gray in including this record in his paper on the Ziphioids of European waters. It is clear, however, from the context that Gray is referring to the specimen described by Dumortier ('39) and taken at Ostend, Aug. 21, 1835. Of this whale, Dumortier relates that it was kept alive out of water for the space of two days but could not be prevailed upon to eat the moistened bread that was offered it! Frequently it gave vent to loud bellowings that resembled the lowing of a cow. Grieg ('98) is able to confirm this testimony as to the possession of a voice by this species, for he states that the female stranded at Karmö in 1895, lowed like a calf that is being slaughtered.

It is clear, then, that *Mesoplodon bidens* is certainly known from the North Atlantic only, between the latitudes of 39° N. (Atlantic City, N. J.) and about 60° N. (Shetland). That it is probably not gregarious has been pointed out by previous writers, and its presence in the colder months at the northern part of its known range has been taken to indicate that it is not migratory, at least in so clear a manner as is the bottle-nosed whale (*Hyperoödon ampullatum*). The fact that so large a proportion of the stranded specimens has been taken on the coasts of islands is indicative of the pelagic habitat of this species as contrasted with certain of the porpoises that often frequent the shallower waters along the coasts.

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FRESH-WATER RHIZOPODS OF NANTUCKET

JOSEPH A. CUSHMAN

During the spring of 1905 collections were made from the bodies of fresh water on the island of Nantucket, Mass., by several members of the Nantucket Maria Mitchell Association. This material was turned over to me for examination. A portion of it was made up of the sediment squeezed from submerged sphagnum. This, as was to be expected, seemed to be the richest in Rhizopods and contained many more species and individuals than the material from the bottom of the larger ponds. Certain species seem to be very limited in their distribution on the island, often occurring in but one of the collections out of the fifty or more examined. In such cases, however, there was usually an abundance of specimens of the species in that one collection. Other forms which were to be expected here were not met with at all. Of these Hyalosphenia was the most striking genus, as it usually occurs in just such material. Nearly all of the species found were of small size for their respective species and may be compared with the specimens noted by the writer and Mr. Henderson from the alpine region of the White Mountains (*Amer. Nat.*, vol. 39, March, 1905, p. 155). The cause of this minimum size in the case of the Nantucket specimens is hard to explain unless for some reason there is not sufficient nourishment for them, but this does not seem to be a reasonable explanation since the ponds are well supplied with minute algæ, especially desmids and diatoms. For certain of the records I am indebted to Mr. W. P. Henderson. The following species were found: —

1. **Arcella vulgaris** Ehrenberg. Breadth 52–55 μ; height 21–23 μ; aperture 12–14 μ.

Common. Hummock and Gibb's Ponds and from bog moss.

2. **Arcella discoides** Ehrenberg. Breadth 46–75 μ; height 20–25 μ; aperture 8–19 μ.

Common, but of small size. Hummock and Sesacha Ponds and from sphagnum in different parts of the island.

3. **Centropyxis aculeata** Stein. Breadth 65–72 μ; height 30–38 μ; aperture 11.5–18 μ.

Of small size. Common in Hummock Pond and in sphagnum swamps.

4. **Centropyxis aculeata ecornis** Ehrenberg. Length 94 μ; breadth 78 μ; aperture 26 μ. From sphagnum.

5. **Quadrula symmetrica** Schul. Length 68 μ; breadth 38 μ; aperture 13.5 μ.

This species occurred but once and then in considerable numbers. It was from bog moss material near the town. The specimens were very uniform in size and were small.

6. **Difflugia globosa** Dujardin. Diameter 58–65 μ. Hummock Pond.

7. **Difflugia pyriformis** Perty. Length 90–102 μ; breadth 45–54 μ; aperture 21–24 μ.

Small. Common in Gibb's and Wigwam Ponds and in sphagnum.

8. **Difflugia acuminata** Ehrenberg. Length 125–168 μ; breadth 40–71 μ; aperture 12–27 μ.

Of small size. Wigwam Pond and from bog moss.

9. **Difflugia corona** Wallich. The only specimens referable to this species were from Wigwam Pond. These were of the usual shape but somewhat undersized and their shells instead of being composed of sand grains were almost entirely made up of diatom frustules. Diameter 112–132 μ; aperture 50 μ.

10. **Difflugia constricta** Ehrenberg. Length 60–87 μ; breadth 36–46 μ; aperture 18 μ. Specimens of this species were found in but one lot of material and in this they were common. They were from bog moss near the town. The specimens were all undersized.

11. **Difflugia lobostoma** Leidy. Length 84 μ; breadth 52 μ; aperture 13 μ. From sphagnum.

12. **Lecquereusia spiralis** Ehrenberg. Length 94 μ; breadth 68 μ; thickness 58 μ.

This species was found in material from the north head of Hummock Pond only. The shells were composed of the peculiar pellets characteristic of this species. The specimens were small for the species.

13. **Euglypha alveolata** Dujardin. Length 90 μ; breadth 75 μ; aperture 23 μ.

This species was met with but once, *viz.*, in material from Wig-

wam Pond. The specimens of this species differ from those of most of the others in being of at least medium size for the species.

14. **Euglypha ciliata** Ehrenberg. Length 44–65 μ; breadth, minimum 20–24 μ; maximum 25–40 μ; aperture, maximum 14.5 μ, minimum 10 μ.

This species may be called common. It was found in material from Hummock Pond and in various collections from bog moss. Unlike the preceding species of this genus the specimens as a rule were undersized.

15. **Assulina seminulum** Ehrenberg. Length 48 μ; breadth 38 μ; thickness 17 μ.

Specimens of this species were found in material from the south end of Hummock Pond. They were of small size.

16. **Heleopera sphagni** Leidy. Length 145 μ; breadth, maximum 100 μ, minimum 48 μ.

This species was found only once but in that material it was common. It was from sphagnum near the north end of Hummock Pond. In size the specimens as a rule were above the average for the species, but were comparatively thin.

17. **Heleopera petricola** Leidy. Length 102 μ; breadth 60 μ; aperture 39 μ. From sphagnum.

18. **Nebela collaris** Ehrenberg. Length 81–150 μ; breadth 58–76 μ; aperture 16–23 μ. From sphagnum.

19. **Nebela caudata** Leidy. A single specimen of this rare species was obtained from sphagnum.

20. **Cyphoderia ampulla** Ehrenberg. Length 110–112 μ; breadth 38–46 μ; aperture 10–12 μ.

In a collection from bog moss near the town this species was abundant, but was not met with elsewhere on the island. The specimens were of very uniform size and small for the species.

21. **Trinema enchelys** Ehrenberg. Length 29–70 μ; breadth 12–34 μ; aperture 4–13 μ. From sphagnum.

22. **Acanthocystis spinifera** Greef. Diameter with spines 75 μ.

Specimens which seemed to be this species were found in material from Reedy Pond. They closely approximate the figures of a species of this genus figured by Leidy without a specific name.

NOTES AND LITERATURE

ZOÖLOGY

Weismann's Theory of Descent.[1] — "When a life of pleasant labor is drawing towards a close the wish naturally asserts itself to gather together the main results, and to combine them in a well-defined and harmonious picture which may be left as a legacy to succeeding generations." Thus does the genial author set forth the aim and motive of his book. And no biologist can fail to be grateful for the publication of these charmingly readable lectures, presenting in two ample volumes the best thoughts of a clear and vigorous thinker. The translation into English has been admirably done.

The early chapters set forth once again the data of evolution and the most striking examples of adaptation, for many of which, in the reviewer's opinion, no other explanation so satisfactory as that of natural selection has ever been offered, and which consequently justify the further elaboration of the theory to which the book is devoted. Four more chapters present the facts of germ cells and fertilization and then the germ-plasm theory is elucidated; criticisms directed against it are answered; various accessory theories, particularly that of intragerminal selection are set forth; and finally its relation to the formation of species is fully discussed.

It is impossible in the space of a brief review to set forth Weismann's standpoint; it is unnecessary, also, for it is already well known to most naturalists. A few words may, notwithstanding, be devoted to his most recent accessory hypothesis upon which he lays the greatest possible stress, that of Germinal Selection. In attempting to explain the gradual disappearance of organs he first hit upon the hypothesis of panmixia but, however satisfactory as a factor of incipient deterioration, it became clear that panmixia could not account for complete elimination. The necessary hypothesis was found in a struggle among the organ-determining germinal particles — the determinants — due to the limitations of nutrition supplied to the germ cells. The

[1] Weismann, A. *The Evolution Theory.* Translated with the author's coöperation by J. A. & Margaret R. Thomson. London, E. Arnold, 1904. 8vo, 2 vols., xvi + 416 and 405 pp.

weaker determinants get less food, grow less well, and consequently become in turn still less capable of nutrition. Once started on the downward path the determinant descends more and more until it is wholly eliminated. Nothing can save the determinant from this fate except the elimination by natural selection of the adults of the strain possessing the deteriorating determinant — and this will only happen when the degenerating organ again becomes necessary to the welfare of the postembryonic organism.

Not only the degeneration but also the upbuilding of an organ can be explained by the hypothesis of germinal selection. For a certain strong determinant once having been selected, it will gather to itself all available nutrition at the expense of the other determinants; it will flourish in the race and will only stop its continual accretions when it produces organs so developed as to be disadvantageous to the active organism.

In criticising this hypothesis one can only admit that it explains so many facts that we hope it will some day be demonstrated. As it is, it stands to-day a bald hypothesis based on numerous probable but unproven assumptions.

Coming now to Weismann's position on the origin of the specific type we find it of interest as being clearly opposed to that of de Vries. Both theories accept the idea of unit characteristics which are represented in the germ by particles. The theories begin to diverge in respect to these particles. De Vries concludes that these particles change suddenly, probably by molecular changes within them, so that a new characteristic arises suddenly and tends thereafter to persist. The characteristic may be modified by selection, but its essential nature cannot be changed thereby. Weismann on the contrary regards these particles as being in a constant state of variation which, when continued long in one direction, will result in the elimination of a character or in its excessive development. Species are originally connected by transition forms as are to-day the terrestrial snails of the Celebes (page 299). Weismann repeatedly emphasizes the idea that all variations are quantitative and that "what appears to us a qualitative variation is, in reality, nothing more than a greater or less" (vol. 2, p. 151). Here then we have clearly set forth the issue between de Vries and Weismann: one maintains that variations of phylogenetic significance are always qualitative; the other, that they are quantitative only. This difference between the two schools would seem to be a qualitative one. But alas for the peace of mind of him who seeks clear distinctions, the quantitative may produce the qualita-

tive, as Weismann points out (vol. 2, p. 152)! He says, a cell changes its *constitution* (*i. e.* undergoes a qualitative change) when "the proportion of the component part and chemical combinations" is disturbed, "when, for instance, the red pigment-granules which were formerly present but scarcely visible increase so that the cell looks red. If there had been no red granules present, they might have arisen through the breaking up of certain other particles — of protoplasm, for instance, in the course of metabolism, so that, among other substances, red granules of uric acid or some other red stuff were produced. In this case also the qualitative change would depend on an increase or decrease of certain simpler molecules and atoms constituting the protoplasm molecule." The foregoing quotation sets forth clearly Weismann's conception of the way in which a wholly new character may arise and I imagine that de Vries would accept the hypothesis. They would differ only as to whether there was at first a great chemical change or a slight one increasing with successive generations. Thus the essential difference between de Vries and Weismann shows itself to be one of degree only.

C. B. D.

The Oyster.[1] — A very fascinating book presenting in a thoroughly scientific, yet in a readable and popular style the complete development and anatomy of the oyster, the possibilities of oyster culture, the cause of the decline in our oyster industry, and the remedy.

One can hardly realize that since statistics have been kept (1865), there have been taken from the Chesapeake Bay, upwards of four hundred million bushels of oysters. "This inconceivably vast amount of delicate, nutritious food has been yielded by our waters without any aid from man. It is a harvest that no man has sown; a gift from bounteous nature."

This great productiveness shows how favorable this body of water is for the oyster, and what might be done under judicial management and culture. It is doubtful if the present areas of oyster beds (about two hundred square miles) can ever regain their former prestige even if they could be utilized to the best advantage by culture. The demand has continued and will continue to outgrow the supply. The area occupied by the natural beds, however, covers but a small por-

[1]Brooks, William K. *The Oyster. A Popular Summary of a Scientific Study.* Second and revised edition, with introductions by Daniel C. Gilman and Ira Ramsen. Baltimore, Johns Hopkins Press, 1905. 12mo, 225 pp., illus.

tion of the bottom suitable for oyster-farming, "and it is safe to estimate the total area of valuable oyster-ground in our state at one thousand square miles." If this vast area could be properly developed, there should be a good supply for years to come. The author points out clearly what should be done, and we trust he will have the coöperation of every intelligent man in saving and redeeming this great industry.

C. W. J.

Sea-shore Life.[1]—Dr. Mayer has presented to the public a popular work which, while not without merit, shows a carelessness in arrangement and constant misstatement of facts which we hardly expect in these days when accuracy and precision of classification are considered of paramount importance.

The book presents a truly attractive appearance, and the figures with few exceptions are new and really valuable. The closing table of references seems well chosen.

The text, however, is the part which gives most evident signs of hasty preparation. The sections dealing with "Jellyfishes and Hydroids" and with "Sea Anemones and Corals" reveal no startling peculiarities, nor, except for rather unimportant details, do the following sections until we arrive at that entitled "The Crustaceans." Here the arrangement is startling indeed. Under the subheading "The Barnacles," the following genera are discussed and figured: Balanus, Coronula, Lepas, *Homarus*, *Palinurus*, and *Alpheus*. "The Crayfishes" follow in a perfectly rational manner. Next come "Shrimps and Prawns." On page 89 we read: "Shrimps are known to science as the Schizopoda!" And now these following genera, presumably Schizopods are discussed Crangon, Palæmonetes, Penæus, Stenopus, and last but by no means the least in this connection, Mysis. Among the "Hermit Crabs" we find Hippa and Squilla. On page 107, Geocarcinus occurs among the "Fiddler Crabs," and under this same main heading the spider crabs and Limulus. Among the molluscs under the heading "The Fresh-water Mussels," we find Pecten, Anomia, and Meleagrina.

We must not, however, presume to be hypercritical. For all its peculiarities this book will probably amuse as many as it leads away from the devious paths of correct scientific classification.

T. B.

[1]Mayer, A. G. *Sea-shore Life. The Invertebrates of the New York Coast.* New York Aquarium Series, No. 1. Published by the New York Zoölogical Society, 1905. 8vo, 181 pp., 119 figs.

Alder and Hancock's British Tunicata.[1]—At last, thirty-eight years after the death of one of the authors (Alder), and thirty-two years after the death of the other, this work on British Ascidians, long known by students of the group to be hidden away somewhere in manuscript, has emerged to the light of day in a well printed volume of 146 pages and 20 plates, dressed in the familiar costume of the Ray Society's publications.

The historical statement by Canon Norman, a personal friend, if I mistake not, of both authors, gives briefly the vicissitudes through which the work has passed both before and since the authors laid it aside for the last time. There is something rather melancholy in a story like this. Pity it is, first having regard for these worthy naturalists themselves, that the fruits of their labors might not have long ago reached the hands of other students of these animals. Thus would a field of knowledge have been enriched, and deserving men could have received the recompense of acknowledgment richly their due, which by this delay has been largely denied them. And the somberness of the picture will be increased a little for many naturalists by the query, with some undoubtedly made more real by personal experiences, as to how far works of their own hands may have a similar fate in store for them.

One of the serious difficulties that has always been encountered by proposals to publish this monograph, Mr. Norman tells, has been the illustrations. A great number of these was left particularly by Mr. Hancock. Of these many were in various stages of elaboration, so that the two-fold problem of what to do with unfinished drawings, and of providing funds for reproducing the large number that was finished had to be met. But little use has been made, we are given to understand, of the unfinished figures. Even so, about 140 are published in the plates, 75 of which are colored; and there are 23 text figures. There can be little doubt that the illustrations will constitute one of the chief values of the work. Most of them are admirably drawn, and the reproduction is in the main good. The habitus figures should be specially useful as a seaside aid to identifying the species.

A historical sketch of the knowledge of the group introduces the work proper. This would have been of high value had it been published long ago; but with the recent extensive studies on the literature by Herdman and Seeleger, this portion of the monograph is made to a considerable extent antiquated.

[1] Alder, J., and Hancock, A. *The British Tunicates.* Vol. I. London, published by the Ray Society, 1905. 8vo, 146 pp., 20 pls.

Hancock's well known paper "On the Anatomy and Physiology of the Tunicata," originally published in the *Journal of the Linnean Society*, 1867, is appropriately reprinted here.

Naturally and very wisely, Mr. Hopkinson has refrained from any revisions of the text beyond what was absolutely necessary to rectify obvious typographic errors. It results from this that in several particulars both as to interpretation of structure, and classification, there is want of conformity to views now held. The most striking thing in this regard is the contention for the molluscan affinities of the tunicates. (The only discussion, however, of this question is that contained in Mr. Hancock's memoir above referred to.) The arguments put forward in support of this view are decidedly interesting reading from a historical point of view, and from the standpoint of now approved criteria of homology. It is surprising that Hancock should have failed even so much as to mention the theory of the vertebrate relationships of the group. One must suppose that at the time of writing this memoir the author had not yet become acquainted with Kowalevsky's important paper on embryology, published the year before. The only clue given us as to what either author's later views were on this fundamental matter, is found in the reference to a paper by Hancock, published in 1870, "On the Larval State of Molgula" etc. Here the author concluded that since there are two distinct modes of development in closely allied genera of the Tunicata, the tadpole condition is non-essential; and he expressed the belief that this fact would influence the theory of the vertebrate relationship of the group.

This volume treats only of the genus Ascidia, in the systematic part, as the genus was then understood. Thirty species are regarded as "good," and five varieties are recognized.

Although the volume is numbered *one*, I see no indication that another is to follow.

It is certainly well that this work is now published, but as certainly it would have been much better could it have been done long years ago.

W. E. R.

Schillings's With Flash-light and Rifle.[1]—The rapidity with which the larger mammals of Africa are becoming exterminated makes it

[1]Schillings, C. G. *With Flash-light and Rifle. Photographing by Flash-light at Night the Wild Animal World of Equatorial Africa.* Translated and abridged by Henry Zick, Ph. D. New York, Harper Brothers, 1905. 8vo, xiii + 421 pp., illus.

imperative that no time be lost in procuring specimens for study and in investigating their habits. Schillings, a German hunter-naturalist, is one of several explorers who in recent years have made expeditions into the Dark Continent and have brought back valuable collections of its rich fauna.

Four expeditions were made into German East Africa by Schillings, and a large number of carefully prepared specimens of the more important game mammals were secured and brought to Berlin for the imperial museum. Several new species have been described from this material (mainly by Matschie) and many others have been forms that are very rare in collections. The present work is mainly an account of the experiences of Herr Schillings during these four journeys into the African wilderness, and is translated and abridged by Henry Zick from the original *Mit Blitzlicht und Büchse* (1905).

The chief feature of the book is the large number of photographs of these animals in their natural surroundings, taken by the author during his three last expeditions. Many of these pictures are remarkable and extremely valuable, taken at night by flashlight as the animals came to the water-holes to drink. Other views were obtained by means of a telephoto lens and illustrate a number of the antelopes and other day-feeding species. Those of the giraffe, the zebra, the lion, and the leopard are particularly noteworthy. Many of the photographs, however, are altogether too indistinct to be of any value, though from an impressionist's standpoint they may pass as pictures. These less satisfactory views have been largely omitted from the English edition, however.

While the photographs are the main feature of the book and by themselves are of permanent value, the narrative is also of interest as a popular treatise on the habits of the species dealt with. A number of notes on the larger mammals are recorded in the course of the narrative, such as the blending of the black and white striped zebras with "the colors of the steppe, so that they are hard to distinguish even at close range" and "under certain lights they appear gravish." That lions at certain times of the year may be found in "troops" of as many as seventeen the author has had personal proof. It is also true that the lynxes of our own country may at times be found in packs although a recent nature writer has dogmatically denied this. The versatility of the long-necked Waller gazelle is shown in its habit of standing on its hind legs, after the manner of goats, in order to increase the vertical extent of its feeding range. In addition to chapters on the rhinoceroses, the elephant, the lion, the giraffe, the zebra, antelopes, and the smaller

carnivores, the latter part of the book deals particularly with the inhabitants of the country and the difficulties that confront the explorer.

The translation is in the main good, though marred here and there by a grammatical error and by a certain looseness of expression, as where scorpions are termed "reptiles," and hippopotami are familiarly spoken of as "river hogs"; the use of capitals for the authority of Latin names seems also to have afforded a stumbling block. An index might have added to the usefulness of the book.

G. M. A.

Notes.— *Recent Extension of the Range of the Green Crab.* About the year 1892 or 1893, I first began to notice at Cohasset, Mass., an occasional specimen of a green crab. These crabs were about two inches in diameter and were seen at low tide on the mud flats about our float in company with *Cancer irrorata*. From that time on I noticed a gradual increase in their numbers but thought nothing of it until 1902, when a reference to a "green crab" in a physiology lecture made me wonder if the crab which had recently become so abundant at Cohasset was the same as that experimented upon. On submitting specimens to Dr. Walter Faxon for determination, I learned that they were *Carcinides mænas*, a species that was not believed to occur north of Cape Cod. In the course of the summer I collected specimens at the following additional localities: Nahant, Lynn, and Ipswich, Mass., and Kittery, Maine. In the same year (1902) it was collected at Manomet Point, Mass., by Mr. J. A. Cushman, and a record of its occurrence at Portland, Maine, was obtained by Dr. Faxon. Miss Mary J. Rathbun in her "List of New England Crustacea," gives the following additional localities in Maine: Harpswell; New Meadows River, near Harpswell; and Eagle Harbor, Casco Bay; all, I believe, based on records obtained shortly previous to 1904.

The next spring, 1904, I determined to find out just how far to the eastward the green crab had reached, but gave up the undertaking after several attempts to procure specimens from Cohasset had proved unsuccessful and after hearing from Kittery that there were practically none to be found there. The winter of 1903-04 had been unusually severe along the shore and the ice consequently very thick. It had scraped every bit of eel grass from off the mud flat at the edge of which the year before I had been able to find an abundance of green crabs and it had probably killed off the crabs along with the eel grass. During the summer I made careful search for more specimens of Carcinides at every locality where I collected and especially at Cohas-

set, but did not find so much as a dead carapace. Mr. Cushman, however, after considerable hunting, managed to secure a few living specimens at Manomet Point. Farther north they seem to have been for the time exterminated.

It is unfortunate that accurate dates cannot be given for the first appearance of this crab at the various stations where it has been taken north of Cape Cod. All the data I can offer on this point are: (1) my impression that they first appeared at Cohasset about 1893; (2) the statement of Mr. Stephen Decatur that he began to notice them at Kittery, Maine, at about the same time; (3) the negative evidence that the species is not included in Professor Kingsley's "Invertebrata of Casco Bay" published in 1901; and (4) the fact that my uncle, Dr. W. S. Bryant, who did considerable collecting and dredging at Cohasset about twenty years ago, had never seen them there.

From these data it appears that the extension of the green crab's range from Cape Cod to at least as far north as Kittery, Maine, occurred very rapidly; that it worked its way slowly along the shore from the neighborhood of Kittery; and that it is not yet permanently established north of Cape Cod.

At Cohasset this last summer, 1905, I found a few dead immature specimens washed up, and on November 19, 1905, Mr. T. Barbour and I collected several living specimens, some nearly full grown, in tide pools on one of the other reefs. There is hope, therefore, that it may again, after a few favorable seasons, become common north of Cape Cod.

The green crab is found in tide pools, along the edge of mud flats, on beaches, and under overhanging rockweed. It does not seem to burrow in sand or mud as does Cancer, when it is left by the tide. It is therefore easily detected and its presence or absence should be noted by everyone who has the opportunity to observe the fauna of our northern New England coast.

OWEN BRYANT

The Pelvic Region of the Porpoise. Because of the degeneration of the pelvic girdle in the porpoises and other cetaceans, it has been impossible on purely osteological grounds to state with precision which vertebræ in these animals correspond to the sacral vertebræ of other mammals. Knauft (*Jen. Zeitschr. f. Naturw.*, vol. 40, pp. 253–318) has attacked this problem from the standpoint of the spinal nerves and has shown that the vertebral column is so related to the lumbo-sacral plexus in the porpoise that instead of possessing 14 lumbar vertebræ as has been generally assumed, this animal has

only 6 and that consequently its sacral vertebræ are much more anterior in position than has heretofore been supposed.

G. H. P.

Adaptations in the Arteries of the Horse. Bärner (*Jen. Zeitschr. f. Naturw.*, vol. 40, pp. 319–382) in a study of the thoracic and abdominal arteries of the horse has shown that the structure of the arteries varies with the blood pressure, the mechanical relations to the surroundings, and the functional relations of the vessels. As the blood pressure decreases in the more distant vessels the arterial walls become thinner and take on more the character of muscular tubes. Where arteries receive support from surrounding parts, as for instance where the aorta pierces the diaphragm, their walls are thin. Finally adaptations are to be seen where special conditions exist; thus the vertebral artery has its elastic elements unusually developed in relation to a demand for the utmost freedom of movement in the horse's neck.

G. H. P.

Two New Chipmunks. Dr. C. H. Merriam (*Proc. Biol. Soc. Wash.*, June, 1905) describes two new chipmunks of unusual interest. One of them, called *Eutamias amœnus operarius*, is the common little four-striped species of the Boreal zone in Colorado. It has been referred to Say's *E. quadrivittatus*, but that species lives in the foothills, and the mountain form is actually nearest to *E. amœnus* of the Californian Sierras. In view of the widely severed habitats of the forms *operarius* and *amœnus*, and the absence of any evidence of intergradation, it would seem that the Colorado animal should rather rank as a full species, *Eutamias operarius*. The other new chipmunk is *E. hopiensis*, an unusually handsome form from the Painted Desert, Arizona.

T. D. A. C.

The Ant Genus Liometopum. Dr. W. M. Wheeler (*Bull. Amer. Mus. Nat. Hist.*, Nov., 1905), gives an interesting revision of the genus Liometopum, as found in North America, with a discussion of the habits of the species. The geographical distribution of Liometopum is of especial interest, as it is one of those types which may be designated palæoboreal; that is to say, it appears to have had a boreal distribution in times past, but has now been driven south, where it persists, with few representatives, in the southern parts of the temperate zones of both hemispheres. Herein it reminds one somewhat of the butterfly genus Parnassius, but it differs from that in the smaller

number of species, and the much less alpine habitat. The species are three, so far as known: *L. microcephalum* of southern Europe, *L. lindgreeni* of Assam and Burma, and *L. apiculatum* (with varieties or subspecies *occidentale* and *luctuosum*) of western North America. In New Mexico *L. apiculatum* ascends to about 8000 ft., and in Mexico even somewhat higher. T. D. A. C.

Ichthyological Notes.— In the *Memoirs of the New South Wales Naturalists' Club*, (no. 2, 1904), Mr. Edgar R. Waite gives a most useful catalogue of the fishes of that State, with reference to the descriptions of each species. Mr. Waite has adopted a modern sequence in his classification and the names adopted by him show a praiseworthy attention to the necessary rules of nomenclature. Five hundred and twenty-six species are enumerated, most of them occurring in the harbor of Sydney.

In the *Records of the Australian Museum*, 1904, vol. 5, Mr. Waite has a useful review of the gobies with separate ventrals, known as Eleotrids, found in the waters of New South Wales. In another paper in the same *Records*, Mr. Waite discusses the breeding habits of the Fighting Fish, *Belta pugnax*.

In the *Transactions of the New Zealand Institute*, Professor W. B. Benham of Otago University describes a new species of the great pelagic Oar-fish, under the name of *Regalecus parkeri*.

In the *Meddelelser fra Kommissionen for Havundersögelser*, of Denmark (vol. 2, no. 7, 1905), Dr. Adolph Severin Jensen gives a monographic account of the ear-stones of fishes dredged in the "Polar Deep." He develops the fact, hitherto unknown, that otoliths in great quantities are deposited in the northern seas at the present time. Many of these belong to the small codfish, *Micromesistius poutassou*, a fish not properly reckoned as arctic.

In the *Bulletin of the Bureau of Fisheries for 1904* (vol. 24) Mr. Frederick A. Lucas discusses the osteology of the Tile-fish, *Lopholatilus chamæleonticeps*, a singular fish of the depths of the Atlantic. He finds the family Latilidæ, to which it belongs, well defined, and well separated from Malacanthus and from Bathymaster, which have been wrongly associated with it. In the same *Bulletin*, Mr. C. E. Silvester discusses the blood-vascular system of the Tile-fish.

In an elaborate paper in the *Proceedings of the Washington Academy of Sciences*, William F. Allen, of Stanford University, describes

in great detail the circulatory system in the fishes with mailed cheeks, or Loricati. Among other things he shows that the Ophiodontidæ and the Zaniolepidæ, should be separated, as dis inct families, from the Hexagrammidæ.

In the *Memoirs of the New York Academy of Science*, (vol. 2, 1905), William E. Kellicott gives an elaborate and useful account of the development of the vascular and respiratory systems of the dipneustan genus, Neoceratodus. He calls this genus by the same name as its extinct ancestor or predecessor, Ceratodus.

In the *Bulletin of the Illinois State Laboratory of Natural History*, Dr. S. A. Forbes and R. E. Richardson describe a new Shovel-nosed Sturgeon from Illinois River, under the name of *Parascaphirhynchus albus*. This species is found mixed with the ordinary Shovel-nose, *Scaphirhynchus platorhynchus* in the proportion of about one to five hundred. The new genus has the belly and breast naked, the ribs twenty or twenty-one. In Scaphirhynchus, the belly is mailed, the ribs ten or eleven only.

In the *Bulletin of the United States Bureau of Fisheries for 1904*, Mr. Chancey Juday, of the University of Colorado, records the species of fishes in Boulder Creek, twenty-five in number, one of them, *Leuciscus evermanni*, being new to science.

In the same *Bulletin* (vol. 24, 1904) Professor Kakichi Mitsukuri of the Imperial University of Tokyo, discusses the domestication or breeding of various fishes, turtles, clams, etc., in Japan. His account of the aberrant forms of the gold-fish, *Carassius auratus*, is especially interesting. About thirty monstrous forms are figured.

In the same *Bulletin* (vol. 24, 1904) Dr. D. S. Jordan and Surgeon J. C. Thompson give an account of the fishes taken by the latter while stationed at the Tortugas in Florida. Two hundred and eighteen species are enumerated, several of them not previously taken in the waters of the United States. New species are: *Holocentrus tortugæ*, *Eviota personata*, *Gnathypops aurifrons*, and *Execestides egregius*, the latter a new genus of Uranoscopidæ. A new genus, Etelides is based on the fish called *Anthias aquilionaris*. It differs from Etelis in the naked jaws, and the union of the two dorsal fins.

In a volume on *The Bahama Islands*, by Dr. George B. Shattuck (Baltimore, 1905), Mr. Barton A. Bean contributes an annotated list of the fishes known, with a number of excellent colored plates, the work of Mr. A. H Baldwin.

In the *Report of the Commissioner of Fisheries for 1904*, Professor John O. Snyder, of Stanford University, discusses the distribution of river fishes about San Francisco Bay. He shows also that *Leuciscus caurinus* of Richardson is a true Leuciscus, and a species distinct from *Mylocheilus lateralis*, hitherto supposed to be the same. *Ptychocheilus grandis* of the Sacramento is also, as Agassiz supposed, distinct from *P. oregonensis*, of the Columbia.

Mr. T. Kitahara (*Annot. Zoöl. Jap., for 1904*) of the Japanese Bureau of Fisheries corrects the nomenclature of some of the trout and salmon of Japan, as given by Jordan and Snyder in 1902. He shows that the "Ito" should stand as *Hucho perryi*, and the "Masu," as *Salmo masou*. The "Iwana," *Salvelinus pluvius*, he regards as identical with *Salvelinus malma*.

Jordan (in the same *Annotationes*, and in the *Proc. U. S. Nat. Mus.*, vol. 27) reviews Mr. Kitahara's paper, recognizing the following species of Salmonidæ in Japan:—

Oncorhynchus nerka (Walbaum); Beni-masu.
Oncorhynchus milkschitch (Walbaum); Gin-masu.
Oncorhynchus keta (Walbaum); Shake or Sake.
Oncorhynchus gorbuscha (Walbaum); Karafuto-masu.
Salmo masou (Brevoort); Masu, Ame-no-uwo, Yamabe.
Hucho perryi (Brevoort); Ito.
Salvelinus malma (Walbaum); Iwana, Ame-masu.
Salvelinus kundscha (Walbaum).
Plecoglossus altivelis (Schlegel); Ayu.

The king salmon, *Oncorhynchus tschawytscha* (Walbaum), has been since recorded from the northern part of Hokkaido, in a letter from Mr. Kitahara. Mr. Kitahara also notes the capture of *Salmo rivularis*, the California Steelhead Trout, (wrongly called *Salmo gairdneri*), off the northern part of the main island of Hondo. These two species should be added to the Japanese list.

The most elaborate faunal monograph yet published by the Bureau of Fisheries, and one of the most beautifully illustrated volumes in existence is the report of Jordan and Evermann on the fishes of Hawaii, published as part of the *Bulletin* of the United States Fish Commission for 1903, the last bulletin issued before the change of the name of the Commission to that of the Bureau of Fisheries.

In this volume are described in full four hundred and thirty-nine species of Hawaiian shore fishes, nearly all of which are admirably figured. Especially noteworthy are the seventy-three colored plates

taken from life in Honolulu and Hilo. Most of these are the work of C. B. Hudson and A. H. Baldwin. Captain Hudson's paintings, made in oil, from living fishes in the aquarium, here perfectly reproduced, constitute beyond question, the finest series of fish portraits ever made by any artist. The wonderfully rich fish fauna of the Hawaiian Islands is now one of the best known in the world.

This fauna is frankly and entirely tropical and almost all the species belong to genera found in the South Seas. The species are, however, in large part different. Of the four hundred and thirty-nine species recognized, two hundred and thirty-two are confined, so far as known, to Hawaii; one hundred and forty-two are found also in Samoa and Fiji; fifty-three are common to Hawaii and Japan, and thirty-four to Hawaii and the offshores of Mexico. The singular isolation of Hawaii, which, so far as fishes are concerned, has no parallel among other tropical island groups, may be due in part to the directions of the ocean currents. These currents seem to play a large part in the transportation of species, by floating young fishes from place to place.

The collections on which this volume is based have been made by the authors, by Oliver P. Jenkins, the first to collect on a large scale in Hawaii, by Charles H. Gilbert, John O. Snyder, Walter K. Fisher, Charles C. Nutting, Michitaro Sindo, and others.

Part 2, of the same *Bulletin*, issued as a separate volume, contains an account of the fishes taken about Hawaii in the deep-sea work of the *Albatross*. This volume is by Dr. Charles H. Gilbert, who was naturalist in charge on the *Albatross* in 1902.

About eighty species were obtained in the deep seas. Nearly all of them are new, an addition to our knowledge of fishes with few parallels in the records of deep-sea dredging. Many new genera are included, and a considerable number of the offshore genera of Japan have their range extended to Hawaii. Among these are Pegasus, Aracana, Gadomus, Hoplichthys, Melanobranchus, Lophiomus, Calliurichthys, and Polymixia.

This volume is to be commended for the careful accuracy of the descriptions and for the excellence of the plates.

The Philosophical Institute of Canterbury in New Zealand publishes an index to the New Zealand Fauna by Captain F. W. Hutton. In this volume is a list of the species of fishes known — without synonyms or references, the nomenclature being apparently carefully considered.

In the *Proceedings of the Academy of Natural Sciences at Philadelphia* (1905) Henry W. Fowler publishes a number of papers on rare or little known species of fishes in the museum of the Academy. One of these treats of fishes of Borneo, with a number of new genera and species; another of Arctic fishes, from Port Barrow; another, in connection with Dr. Benjamin Sharp, on the fishes of Nantucket. Two others treat of rare or little known forms allied to the Mackerel. A new subgenus, Sierra, is proposed for *Scomberomorus cavalla*; another, Lepturacanthus, for *Trichiurus savala*. *Caranx ruber* becomes the type of Elaphrotoxon and Vexillicaranx is typified by *Caranx africanus*. Rhapiolepis is based on *Scomberoides tol*. The Pilot-fish of the Pacific, found in Hawaii and Japan is described as *Naucrates polysarcus*, the type being from the West Coast of Mexico. If the species is valid, some one of the older names, given to Pacific specimens may belong to it.

In the *Proceedings of the United States National Museum* (vol. 28), Dr. Theodore Gill has a number of short papers on new points in ichthyology. *Prionotus stearnsi*, a smooth-headed gurnard from Florida, is the type of a new genus, Colotrigla. The insertion of the pectoral fins furnishes the chief distinctive peculiarity. Simopias is a new name proposed as a substitute for Pelor, preoccupied, and Rhinopias is proposed as the generic name for the singular *Scorpæna frondosa* of Martinique. The subfamily Pelorinæ becomes Inimicinæ, for the genus Inimicus. *Neosebastes entaxis*, a Japanese fish, is properly removed from Neosebastes to become the type of Sebastosemus Gill.

In the *Report of the United States Commissioner of Fisheries*, Dr. Gill gives an interesting historic review of the ichthyology of Massachusetts. Attention is called especially to the number of waifs, young fish from the tropics, found each year, where the Gulf Stream reaches the coast of Massachusetts.

In the *Proceedings of the United States National Museum* (vol. 28, 1905), Messrs. Jordan and Seale discuss the collection of fishes brought by Professor Bashford Dean from the island of Negros in the Philippines. One hundred and eighteen species, mostly small fishes from the coral reefs, were obtained, of which eighteen are new to science. The fish fauna of the Philippines is essentially that of the East Indies, with a dash of forms from the shores of Hindostan.

In the same *Proceedings*, Dr. Peter Schmidt of St. Petersburg discusses the huge Japanese Snail-fish, *Trismegistus owstoni*, and con-

cludes that its peculiar prickles do not justify generic separation from Liparis.

In the *Smithsonian Miscellaneous Collections* (vol. 45, 1904), *Hemibarbus joiteni*, a large chub from China, is described by Jordan and Starks.

In the *Proceedings of the United States National Museum*, (vol. 28, 1905), Dr. C. H. Gilbert and Surgeon J. C. Thompson discuss certain rare fishes collected by Dr. Thompson in Puget Sound. Two new species, both sculpins, are described: *Stelgidonotus latifrons*, and *Malacocottus kincaidi*, the first a type of a new genus. *Artedius asperulus* Starks proves to be the young of *Astrolytes fenestralis*.

In the same *Proceedings*, Messrs. Jordan and Starks discuss the fishes collected by Pierre L. Jouy on the coasts of Korea. Seventy-one species were obtained, a considerable number of which are new to science. The shore fishes are essentially those of Japan; the river fishes are nearly all new to science and of Chinese types.

In the *Annotationes Zoölogicæ Japonenses*, (vol. 5, 1905), Hans Sauter of Yokohoma describes a new fish from Japan, of the family Ateleopodidæ, under the name of *Ijimaia döfleini*. The genus Ijimaia differs from Ateleopus in the rather slight character of the shortened ventrals, and in the position of the mouth.

In the *Sitzungsbericht der Gesellschaft der naturforschender Freunde*, 1905, Mr. P. Pappenheim discusses the genera of Sturgeons, referring the Asiatic species of shovel nose, (Kessleria=Pseudoscaphirhyncus,) back to the American genus Scaphirhynchus. There is no obvious justification for this arrangement.

A. C. MacGilchrist (*Ann. Mag. Nat. Hist.*, ser. 7, vol. 15, 1905), describes a new genus, Dysalotus, (*D. alcocki*), allied to Chiasmodon, from South Africa.

Other short papers in the same *Annals* are by Mr. C. T. Regan, of the British Museum. From Tequesixtlan, Mexico, is described a new goby, *Cotylopus punctatus*. *Pseudoxiphophorus pauciradiatus* is held to be a valid species and a new "variety," whatever that may mean, is recorded from San Domingo de Guzman as *Pseudoxiphophorus bimaculatus* var. *tæniatus*.

Another paper deals with the genera of Asiatic catfishes, Parexostoma, Chimarrhichthys, and Exostoma. Still another describes two new fishes from the Inland Sea of Japan, unfortunately without indication of exact locality, and a new minnow from Lake Biwa.

In another paper, Mr. Regan defends his treatment of the genus Arges against strictures made by Messrs. Evermann and Kendall.

Useful revisions of certain South American genera of Cichlidæ are also given by Mr. Regan. It is not clear that any useful purpose is served by changing the spelling of Crenicara, to Crenacara. The whole tendency in nomenclature at present is to let a name stand as it is written. Purism breeds confu ion.

Dr. Rudolph von Ihering in the same journal describes four mailed catfishes from Brazil, additional to those contained in the monograph of Mr. Regan.

In the *Revue Su isse*, (vol. 13, 1905), Mr. Regan describes six new species of fishes in the museum of Geneva. One of these, *Sciæna* (*Bairdiella*) *bedoti* is from Cuba.

In the *Proceedings of the Bombay Natural History Society*, Mr. Regan describes a number of new species from the Persian Gulf with a series of excellent figures.

In the *Comptes Rendus of the Sixth International Congress*, 1904, Dr. Jacques Pellegrin records a small coll ction of fishes from Lake Tchad, the first made in these waters. Its fauna is, however, not distinct from that of the great rivers of Central Africa. Dr. Pellegrin also describes the hatching of the eggs of the perch-like fish, *Tilapia galilæa*, in the mouth of the mother.

In the *Report of the Commissioner of Fisheries for 1904*, Ulysses O. Cox gives a revision of the cave fishes, Amblyopsidæ, of North America, with figures of most of the species. At about the same time, Dr. C. H. Eigenmann describes two new species of cave fishes, (*Biol. Bull. Ind. Univ.*, vol. 8, 1905). These are *Typhlichthys wyandotte*, from Corydon, Indiana, and *T. osborni* from Horse Cave, Kentucky.

In the *Proceedings of the Washington Academy of Science*, Dr. C. H. Eigenmann and David P. Ward give an excellent monographic review of the South American fishes constituting the family of Gymnotidæ. A few new generic names are proposed.

Dr. Robert von Lendenfeld (*Bull. Mus. Comp. Zoöl.*, 1905) describes in detail the radiating organs of deep-sea fishes, with a series of admirable plates. These organs, known as luminous organs or glands, are for the purpose of radiation of waves of light, ultra red, perhaps, or in some cases of electricity.

In the *Report on Norwegian Fishery Investigations*, Dr. Robert Collett describes the species taken in the cruise of the *Michael Sars* in the North Sea. Valuable notes accompany the list of species. A new subgenus, Bathyalopex, is proposed for *Chimæra mirabilis* and for the Japanese species, *Chimæra mitsukurii*, in which the anal is not notched.

In anothe paper, Collett describes a new lantern-fish, *Lampadena chavesi*, from the Azores.

In two volumes, large quarto, under the title of *A Guide to the Study of Fishes*, Henry Holt and Co. publish a general account of fish life, fish structure, and fish classification by Dr. D. S. Jordan. This work is doubtless the most elaborate yet published on this topic. It is beautifully printed and fully illustrated, and the author has tried to put into it all that he knows about fishes which can have an interest to naturalists and to the cultivated public generally. Works of similar scope but less detailed in their treatment, are Dr. Günther's *Introduction to the Study of Fishes* and the volume on fishes in the Cambridge Natural History, this last work appearing almost simultaneously with Jordan's *Guide*.

Dr. C. R. Eastman (*Mém. Soc. Géol. de France*, vol. 13, 1905) treats exhaustively of the Eocene fishes of Monte Bolca in the Museum d' Histoire Naturelle de Paris. A number of new species are described and figured. Not much account is taken of the questions of priority, else the preoccupied name, Platyrhina, would not be used for Discobatus of Garman, or Trygon for Dasyatis. Zanclus hardly belongs to or even near to the Carangidæ, and Serranus, Apogon, and Dentex are not nowadays Percidæ. But these are minor issues, in comparison with the elucidation of this earliest of fossil tropical fish faunas having a modern cast.

In the *Report* of the State Geologist of New Jersey for 1904, Dr. Charles R. Eastman contributes a popular account of the significance of fossil remains of fishes. This is followed by a description of species found in the Triassic rocks of New Jersey, with photographic plates of numerous species.

In the *American Geologist*, vol. 24, 1904, Dr. Bashford Dean shows that the Permian fish, Menaspis, may be a Chimæroid.

Mr. L. Hussakof (*Bull. Amer. Mus. Nat. Hist.*, 1905), discusses the fish called *Dinichthys intermedius*, and its probable traits in life.

An interesting and valuable biographical sketch of Peter Artedi, the "father of ichthyology," is published by Einar Lönnberg, as a

memoir in behalf of the Swedish Academy of Science. "Artedi was the first to settle definitely the notion of genus in zoology and to make clear the difference existing between species and variety, to demand a classification on natural principles into classes, orders, etc., based inter alia on comparative anatomical investigation." This address marks the bicentennary of the birth of Artedi, March 10, 1705.

The seventh volume of the *Cambridge Natural History* treating of the "Fishes, Ascidians, etc.," is a most substantial and valuable contribution to our general knowledge of these groups. In this book of 753 pages, the Hemichordata, are treated by Dr. S. F. Harmer, the Ascidians and Lancelets by W. A. Herdman, the lower fishes by Dr. T. W. Bridge, and the Teleosts by Dr. G. A. Boulenger. The excellent account of the structure and physiology of fishes is by Dr. Bridge. Throughout the volume, the treatment of the subject is accurate and dignified, though distinctly technical. The fossil forms, represented by excellent plates, are placed in proper sequence with the living forms. Modern researches in the osteology of fishes have been carefully considered, and in general, more attention has been given to the rules of scientific nomenclature, than in most general treatises on ichthyology. A series of small maps showing the geographical distribution of various groups is an excellent feature of the work. By placing the Cycliæ, Ostracodermi, and Arthrodira in the appendix, Dr. Bridge is enabled to avoid any theory as to the actual relationship of each. The Cladoselachidæ are regarded as the most primitive of the known sharks, and the Crossopterygians as probable ancestors of amphibians, Dipneustans, and the bony fishes, in accordance with the carefully considered theory of Dr. Dollo.

The treatment of the Teleostei by Dr. Boulenger represents long-continued studies on the part of an original and forceful worker. In the main, the general views and the sequence adopted coincide fairly with the classification current among American ichthyologists. This is gratifying, as tradition at the British Museum leads along the old Cuvierian lines. The adoption of the theory of development does away with the sequence which would place the perch as a typical fish at the head of the series. The head of the series of bony fishes must be the most primitive of these forms, and this, all now agree, must be found in the herring-salmon group, called by Cope, Isospondyli.

From these generalized forms, we proceed to those more and more complex. In this, there is no longer much doubt as to the main facts, but there is room for great play of individual whim or taste in the relative sequence of the branches. As a book classification must be

linear, the sequence can be natural in only a very slight degree at the best. Dr. Boulenger prefers a less minute subdivision of families than that adopted by Gill, Cope, and American writers generally. This matter is not a vital one. There is something to be said on either side. In a subdivision too minute the close relation of forms may be lost sight of. On the other hand, by attaching aberrant forms to the nearest family, we often destroy the naturalness of our groups. As the suborders of Teleostean fishes are very unequal in value, very much intertangled, and for the most part incapable of trenchant definition, Dr. Boulenger has been no more and no less successful than others in defining them. The fault lies with Nature, who has not done her part in the elimination of interlocking forms. The emphasis laid on the characters of the Ostariophysi is a step forward, as is also the separation of the Symbranchii from the eels. There seems to be no very good reason for using the term Malacopterygii for the group defined as Isospondyli, as the great majority of the species called Malacopterygii by Cuvier belong to the Ostariophysi and Haplomi. The Haplomi of Boulenger is not a natural group, and more extended study is necessary before we can draw the line accurately between Isospondyli and Haplomi. The suborder Heteromi of Boulenger seems to be unduly extended. The Catosteomi (Lampris and sticklebacks) form an unnatural association, as Dr. Boulenger (p. 627) seems about ready to admit. It appears, however, reasonable to place the pipe-fishes in the same suborder with the sticklebacks. The Percesoces of Boulenger can hardly hold together long. Ammodytes is a jugular fish, the Scombresoces diverge in the direction of the Haplomi, while Polynemus, Chiasmodon, Stromateus, and Anabas, all diverge widely from the mullets and other typical Percesoces, and each in its own way. As a matter of fact, the Percesoces at the best are no farther from the true Acanthopterygii than is Beryx or Gobiesox or Callionymus. Percopsis, placed by Boulenger with the Haplomi, is better separated from everything else, than the members of the Haplomi-Catosteomi-Percesoces-Acanthopterygian series are from each other. But this is the fault of Nature, not of the systematists. Aphredoderus, as Starks has shown, is not a Berycoid fish. The group Zeorhombi (the John Dory and the flounders), indicates an association not yet proved, but on the whole the allocation of families and genera among the perciform types is very satisfactory. The "new University" of Cambridge, to borrow the phrase from the preface to the work, is to be sincerely congratulated on this additional contribution to sound science and scientific method. D. S. J.

(No. 472 was issued April 16, 1906.)

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THE AMERICAN NATURALIST

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CONTENTS

			Page
I.	Observations and Experiments on Dragonflies in Brackish Water	R. C. OSBURN	395
II.	Reactions of *Tubularia crocea* (Ag.)	A. S. PEARSE	401
III.	Pressure and Flow of Sap in the Maple	DR. K. M. WIEGAND	409
IV.	Notes and Literature: *Teaching*, McMurry's Special Method in Elementary Science; *Evolution*, Lotsy's Theories of Descent; *Exploration*, Scott's Voyage of the 'Discovery'; *Botany*, Harris on Anther Dehiscence, Freeman's Minnesota Plant Diseases, Ward's Flowers of English Trees and Shrubs, Notes, The Journals.		455

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OBSERVATIONS AND EXPERIMENTS ON DRAGONFLIES IN BRACKISH WATER

RAYMOND C. OSBURN

WHEN we consider the great variety and extent of adaptation among the insects, and especially when we recall the multitude of aquatic and semi-aquatic species, it seems rather remarkable that none of them has been able to take up marine life. Halobates, one of the Hemiptera, is truly oceanic, a few species of Diptera are known to live in sea water during their larval stage, a few larval forms have been found below high tide where they would be exposed to the sea water for a portion of the time, and a number of adult insects, chiefly beetles, range the shore finding their food when the tide is out.

In brackish water, however, many species are regularly found, belonging to nearly all the insect orders. It is a noteworthy fact that nearly all of these are more commonly found breeding in fresh water and are not peculiar to brackish water conditions.

While the occurrence of dragonfly nymphs in brackish ponds must have been noticed many times by observing naturalists, references in literature are exceedingly scant. Mr. E. A. Schwartz ("Preliminary Remarks on the Insect Fauna of the Gt. Salt Lake, Utah," *Can. Ent.*, vol. 23), found nymphs living in a mixture of salt and sulphurous or fresh water about Gt. Salt Lake, but adds: "The same species were also seen at Utah Lake, which is fresh water"; and the eminent authority on the dragonflies, Dr. P. P. Calvert in his "Catalogue of the Odonata of the Vicinity of Philadelphia" (*Trans. Amer. Ent. Soc.*, vol. 20, 1893) makes the

following statement: "No Odonate nymphs are known to live in salt water, but probably some coast species, such as *Ischnura ramburii* and *Micrathyria berenice* live in that which is brackish."

The writer's attention was first attracted to the presence of dragonflies in brackish water by the discovery that many common Pacific Coast species were breeding abundantly in a slightly brackish pond near Victoria, British Columbia. No estimate of the salinity could be made but it was slight. Again at Wood's Hole, Mass., many common forms were also found living in brackish ponds of varying density. The following list of species noted breeding in brackish water will serve to show what a variety of those ordinarily breeding in fresh water may, if occasion require, live equally well to all appearances in slightly salt water. At Victoria, B. C.: *Enallagma carunculatum, Ischnura pervarva, I. cervula, Aeschna californica, Sympetrum madidum, Mesothemis simplicicollis* var. *collocata, Libellula quadrimaculata,* and *L. forensis.* At Wood's Hole, Mass.: *Lestes unguiculatus, L. rectangularis, Nehalennia irene, Enallagma civile, Ischnura verticalis, Anax junius, Leucorhinia intacta, Micrathyria berenice, Sympetrum rubicundulum, Libellula pulchella, L. auripennis,* and *Plathemis lydia.* These records were obtained partly by identification of the nymphs, partly by rearing the imagos, and partly by collecting the young imagos just after their transformation. The Wood's Hole list represents only seven weeks collecting in July and August and in a very restricted locality so it is highly probable that the list represents only a few of those that may be found in brackish water. Of the above species, only one, *Micrathyria berenice,* is limited in its range to near the coast, and as it also breeds in fresh water in the same region it can hardly be said to be a typical brackish water species.

In order to determine the salinity of water in which dragonflies may live the following experiments and tests were made at Wood's Hole during the summer of 1905. As the work had to be pursued for the most part at odd moments my observations are not as complete as could be wished, and yet they are full enough to be quite significant. My thanks are due the U. S. Bureau of Fisheries for the opportunity to carry on the work while connected with the Wood's Hole Station as temporary scientific assistant.

In the first place, a series of salinometer tests of the water in all the ponds in which dragonfly nymphs were found, was made. Water from four such ponds on Nonnamesset Island and from three on the mainland was tested and in none of them was the density greater than 1.0015, while the average was about 1.0008. These tests were made at a temperature of 72° Fahr. and as the figures have not been reduced the actual density would be considerably greater. It will be noted, however, that water of such density contains but little salt in comparison with that of sea water, which has an average density of 1.026. One pond examined had a density of 1.015 at 72°, but, though dragonflies of several species were seen about this pond, a careful examination revealed no dragonfly nymphs living in the water and it is a safe assumption that the adults came from less saline ponds in the vicinity. Even if oviposition should take place under such conditions it is highly probable, as will be shown by the experiments to be discussed, that no eggs would develop.

Next, the experiment of placing nymphs in saline solutions of various densities was tried. Chiefly the nymphs of *Lestes unguiculatus*, an Agrionid, were used. These were taken from a pond of the density of 1.0012. Those placed in water which was entirely fresh showed no ill effects from the change, and the same is true of those put into saline solutions of low density, up to about 1.003. Beyond this point the larvæ showed increasing signs of irritation. In solutions at 1.005, 1.0075, and 1.01 the nymphs at first wriggled and swam violently, tried to climb up the sides of the aquaria and otherwise gave evidence of much irritation, but they apparently became inured to it after a day or so and lived as well in these solutions as in that in which they were found. Higher solutions were always fatal. In sea water at 1.02 they lived only a few hours, and at 1.015 they showed every sign of discomfort and invariably died within a day or so.

The larvæ of *Ischnura verticalis*, also an Agrionid, of *Anax junius*, an Aeschnid, and of several Libellulids, chiefly *Sympetrum rubicundulum*, showed entirely similar results.

Further experiments on the development of the eggs in brackish water yielded some interesting results tallying well with those made on the nymphs. Eggs of *Libellula auripennis* Burmeister

were taken just prior to oviposition on July 16, 1905. These were placed in solutions of various densities at 75° F. as indicated in the following table with the results noted:—

Density of water	Result
Fresh	hatched July 30
1.001	" " "
1.002	" " "
1.003	" " "
1.004	" " "
1.005	" " "
1.0075	" " "
1.010	" " "
1.015	Failed to hatch, partial development
1.020	" " " no development (?)

A glance at the above table shows that the amount of salinity from fresh water up to 1.010 had no effect whatever on the time of hatching; all hatched out together 14 days after fertilization. The 1.015 and 1.020 cultures were kept under exactly the same conditions but neither developed to the point of hatching. In the former considerable development took place, to the extent that the main structures of the larva were outlined, but in the latter no indications of development could be observed except some cases of questionable segmentation.

No differences could be noted between the larvæ hatched in 1.010 and those hatched in weaker solutions or fresh water and later experiments proved them to be equally hardy.

The young larvæ were now transferred to solutions differing from those in which they had been hatched, in order to test their resistance to density changes at this period. The results tally remarkably with those on the older nymphs and with the hatching experiments. Larvæ hatched in 1.010, 1.0075, and 1.005 solutions when placed in fresh water showed no discomfort and lived as well as those hatched in the fresh water, while those hatched in fresh water stood the change into the above solutions without any noticeable effect. The attempt to run any of them into higher solutions, however, always resulted fatally in a short time. In 1.015 they died in less than a day, in the 1.020 they were killed in

a few hours. Those hatched in the 1.010 solution had apparently gained no further power of resistance but succumbed as quickly as those from fresh water. This test was repeated after two weeks but with the same result, they still were overcome as readily as when first hatched.

The above experiments indicate that there is in the Odonata a very definite barrier to their assumption of marine life, and that this barrier remains unchanged during the life of the individual. That it is the same for all species has not yet been determined, and it may be that forms such as *Micrathyria berenice* which are limited in distribution to the coastline have a higher limit than those species which occur in the interior only. As to the nature of the barrier we are entirely in the dark. It may be that the eggs and nymphs of Odonata are able to prevent the osmosis of salt in solution up to a certain point, but it seems more probable that the metabolism is interfered with only by salt in solution above a certain density. Whether other groups of insects are similarly restricted is also unknown.

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CONTRIBUTIONS FROM THE ZOÖLOGICAL LABORATORY OF THE MUSEUM OF COMPARATIVE ZOÖLOGY AT HARVARD COLLEGE. E. L. MARK, DIRECTOR. No. 178.

REACTIONS OF *TUBULARIA CROCEA* (AG.)

A. S. PEARSE

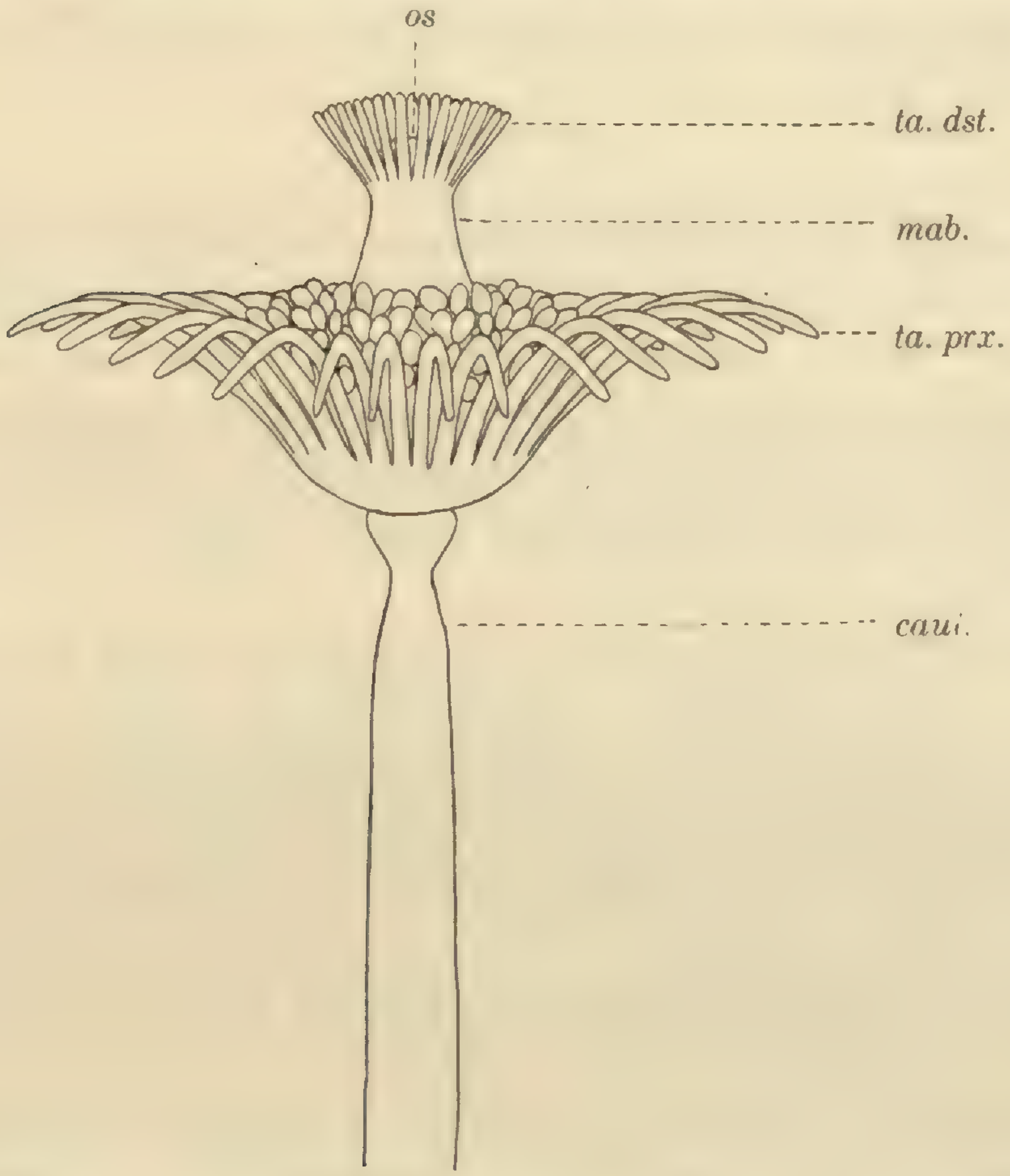
WHILE the reactions of sea anemones and of jelly fishes have been carefully studied, comparatively little is known of those of hydroids. In fact, the only recent paper which deals primarily with this subject is one by Torrey (:04) on *Corymorpha palma*. He found that this hydroid gives well marked reactions to gravity and mechanical stimulation, but does not respond to chemical stimulation.

The work upon which the present paper is based was undertaken at the suggestion of Professor G. H. Parker, and the experiments were carried on at the Laboratory of the United States Bureau of Fisheries at Wood's Hole, Mass. My thanks are due to the director, Dr. F. B. Sumner, for the courtesies shown me at the Wood's Hole Laboratory and to the Museum of Comparative Zoölogy for pecuniary assistance granted from the Humboldt Fund.

The material, consisting of colonies of Tubularia, was scraped from the piles of the wharf at the Fisheries Station and examined in sea water within three hours of the time of collection. The colonies are rather delicate and are easily rendered inactive or killed by unfavorable conditions. Small portions of colonies, containing from twenty-five to fifty polyps, were used in these experiments.

The accompanying figure represents an expanded hydranth of *Tubularia crocea* and a short portion of the stalk upon which it is borne. In a resting hydranth the proximal tentacles (*ta. prx.*) are bent slightly back toward the stalk (*caul.*) and remain motionless except for an occasional sudden movement toward the mouth (*os*), after which they slowly return to their former position. The distal tentacles (*ta. dst.*) are more active and are usually in motion,

bending back and forth singly or collectively. The manubrium (*mab.*) is ordinarily motionless, but may shorten or lengthen and, when stimulated, is capable of bending even to such an extent that



the mouth is brought below the bases of the proximal tentacles. The whole hydranth may be moved by the bending of the stalk, but this action is not of frequent occurrence and it is apparently not called forth in response to direct stimulation.

MECHANICAL STIMULATION

When a proximal tentacle is touched with a needle or pinched, it bends toward the manubrium. The strength of the stimulus influences the response. If the stimulus is weak, there may be no reaction, but if it is strong, the whole circle of tentacles may close up together and press against the manubrium. If the manubrium or the distal tentacles are stimulated in a similar manner, the for-

mer bends toward the point of stimulation and a few or all of the distal tentacles wave about for a short time. If in this process they touch some object, they then close up around the mouth. When the stimulation is very strong, the manubrium shortens and both sets of tentacles close up around it.

The hydranths will submit to considerable mechanical stimulation without reaction. For example, a stream of water forced from a pipette upon an expanded individual will cause no movement unless the current is rather strong.

If a proximal tentacle is pulled vigorously, the manubrium will turn so that the mouth is brought toward the stimulated point and the distal tentacles will open out. However, as each set of tentacles may be made to react independently and without apparent influence on the other set, it seems probable that in this case the manubrium is strained and thus stimulated directly.

The reactions described above are doubtless helpful to the animal in securing food, though they are not perfectly adapted to this purpose. They are not very accurately adjusted to the gathering of food, for the proximal tentacles will always move toward the mouth even when the point of stimulation is on the outer face, in which case they move directly away from what may be food.

Chemical Stimulation

When a proximal tentacle is touched with a piece of meat at any point, it bends toward the mouth. The meat, if it is on the inner face of the tentacle, is pressed against the mouth for a time and then the tentacle slowly returns to its former place. All the proximal tentacles often close up in the presence of meat, but those in contact with it react first and remain closed after the others have opened out, which they usually do quickly. If meat is placed very gently on the proximal tentacles, no reaction takes place and it falls off or remains resting upon them. Sometimes when meat is placed upon them, the bending reaction takes place, but this is so feeble that the meat does not move far enough to reach the distal tentacles and in such cases there is no movement of the manubrium or distal tentacles. When meat comes in contact with the distal tentacles,

however, they bend outward and the manubrium turns them toward the stimulated side. If they then touch the meat, they close up around the mouth.

These reactions make it appear as though the procuring of food depended wholly upon mechanical stimulation, as Torrey has claimed in the case of Corymorpha; but the following experiments have led to a somewhat different conclusion. When a grain of sand is placed on one side of a hydranth,—being allowed to rest upon the proximal tentacles and to touch the distal ones,—and a piece of meat is placed in a corresponding position on the opposite side, the manubrium almost invariably turns toward the meat and the distal tentacles open out. In another experiment meat juice was extracted and filtered. This filtrate has a milky appearance and can easily be seen in water. When it is allowed to flow gently from the mouth of a pipette on the proximal tentacles, no reaction takes place, but as soon as it touches the distal tentacles they expand and the manubrium bends toward the stimulated side. To prove that these reactions are not due to mechanical stimulation produced by particles of solid matter or by currents, the same experiment was tried using powdered carmine in sea water instead of meat juice.

In 15% of the trials (685) with carmine water the mouth was turned toward the stimulated side and the distal tentacles opened out, but when the meat filtrate was used upon the same individuals the turning and opening-out reactions took place in 82% of the trials (717).

A third experiment points in the same direction. If the distal tentacles of an active hydranth are touched several times with a needle, they close tightly over the mouth. If, after a moment, they are touched again with the needle, they remain closed for some time; but if as a second stimulation they are touched in the same manner with a piece of meat instead of a needle, they at once open out and wave about.

From the above experiments it is reasonable to conclude that the distal tentacles, and perhaps the manubrium, are sensitive to a substance or substances contained in meat juice, while the proximal tentacles are not.

The effect of other chemical substances was tested without ob-

taining particularly significant results. When treated with dilute onion juice, quinine solution, or acetic acid, the hydranths closed up for a time, and if the solution was strong enough, they were killed. These substances, unlike meat, produce the same reactions as does strong mechanical stimulation.

Filter paper soaked in meat juice, onion juice, clove oil, or oil of bergamot and held near the hydranth caused no reaction of any part, the animal being apparently insensitive to the resulting very dilute solutions.

Thermal Stimulation

Colonies of Tubularia were placed in glass dishes and the effect of a rise or fall in temperature noted. When the temperature of the water was raised above 25° C. most of the animals were inactive, though two individuals turned the proboscis and opened out the distal tentacles when, at 27.5° C., they were touched with meat. No animal, after having been heated to 26° C. and then cooled again to normal [1] temperature, survived and reacted normally. When the water was cooled to about 10° C. most individuals became inactive to meat, though a few reacted to this form of stimulation even at 0° C. Probably the colonies survive any temperature down to near freezing, as individuals which had been for half an hour in water which was frozen (–2.2° C.) at the bottom of the dish and had a temperature of 1.5° C. at the top, gave the usual reactions thirteen hours later at a normal temperature. In no case did animals survive actual freezing in the ice. In extreme changes of temperature, the proximal tentacles cease to react before the distal ones, and this is what might be expected from the relative sensitiveness of the latter.

Local thermal stimulation was attempted with a bent capillary heated tube, or cooled by a current of water such as Mast (:03) used in his experiments on Hydra. The tube was held near the hydranth but not allowed to touch it. A cold tube (ice water) caused no perceptible effect on any part of the hydranth, but a hot

[1] The average temperature (readings at 8.00 A. M. and 5.00 P. M.) at Wood's Hole during the first ten days in August, 1905, was 19.8° C.

tube caused a restless indeterminate movement of the distal tentacles.

PHOTIC STIMULATION

No extensive experiments with light were attempted. Colonies were placed in the dark and then suddenly illuminated by a 16 c. p. electric light, or a shadow was cast over them after they had been illuminated for some time, but no observable reactions occurred in either case. It was also noted that the colonies grew just as abundantly on the sides of the piles most exposed to light as on those least exposed.

SUMMARY

1. The proximal tentacles of *Tubularia crocea* react to mechanical stimulation by bending toward the manubrium.
2. The distal tentacles react to mechanical and chemical stimulation by bending toward or away from the mouth, and this action may be accompanied by a bending of the manubrium toward the stimulated side.
3. Apparently no part of the hydranth is sensitive to very dilute solutions of meat juice, onion juice, and oil of cloves or bergamot (so called "odorous" substances).
4. The minimum temperature at which reactions occur is 0° C. and the maximum about 26° C.
5. Sudden change from strong light to shadow or from darkness to strong light has no apparent effect upon the animals.

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PRESSURE AND FLOW OF SAP IN THE MAPLE[1]

K. M. WIEGAND

It is with some hesitation that a contribution is here attempted to the already voluminous literature regarding the ascent, flow, and pressure of sap in trees. Work on the maple has reached such a point, however, that it seems desirable to review critically our present knowledge to see which, if any, of our various theories are tenable, in how far, and why.

General Account of Conditions Accompanying Flow

In recent years the phenomenon of bleeding in plant tissue has come to be recognized as a very general one.[2] It has been found to occur in tissues widely different in nature, and under widely different conditions. Perhaps the bleeding of the root, accompanied by root-pressure, is the best known example of this phenomenon. The bleeding of trees in the spring attracted the attention of the early investigators, and has been the subject of considerable wonder and mystery ever since. Although it is a common phenomenon, we know comparatively little about the cause.

In late winter and early spring, if the maple is "tapped," that is, bored with an auger, sap will flow from the wound in considerable quantity, the flow being dependent very largely upon the temperature. Some other trees that bleed in the same way as the maple, though usually not to so great an extent, are *Juglans cinerea*, Cladrastis, Nyssa, and sometimes *Prunus serotina*. Later in the spring, just before vernation, the birch and grape bleed profusely, and, to a lesser extent, also Ostrya, Hicoria, Alnus, Malus, Cratægus, Salix, Ulmus, and perhaps a few other trees.

Investigation of these various trees has shown that they fall

[1] Contributions from the Department of Botany of Cornell University, No. 109.

[2] Wieler, A. "Das Bluten der Pflanzen." *Cohn's Beiträge*, vol. 6. p. 1, 1892.

into two very definite groups as regards the bleeding phenomena, with a different source, and perhaps different cause, for the bleeding in the two cases. Those which, like the maple, bleed early in the spring and are dependent upon temperature, constitute one class, while the late-bleeding ones, like birch and grape, which are not intimately dependent upon the temperature, constitute a class by themselves. This paper is concerned entirely with the first of these two groups, and only a few words will be said about the other group at the close, as a matter of comparison.

Branches cut from certain trees at a low temperature and brought into the warm laboratory often show bleeding from the cut surface. Clark tested sugar maple, white birch, elm, hickory, buttonwood, chestnut, and willow in this respect. The maple soon began to bleed at the rate of 24 drops per minute, while the buttonwood bled 11 drops, and the hickory exuded a little very sweet sap, precisely as in spring. The birch, chestnut, elm, and willow did not flow at all, and were not even moist on the cut surface. I have often repeated this experiment with maple branches. By passing the branch between the flues of a radiator a very vigorous exudation can frequently be obtained. The trees that bleed in this way are usually those in which the vessels are comparatively saturated with sap. According to Clark, a mercurial gauge attached to the end of a frozen branch of sugar maple indicated pressure and suction when the temperature was raised and lowered precisely as it would have done upon a maple tree during the ordinary alternations of day and night in the spring of the year when the sap is flowing.

LATE WINTER FLOW IN MAPLE AND OTHER TREES

Considering its importance from an economic standpoint, the subject of maple-sap flow has received comparatively little attention. In 1874 and 1875 Clark[1] published the results of several years of detailed work upon the maple. These two papers really

[1] Clark, W. S. *The Circulation of Sap in Plants* (*A lecture before the Mass. State Board of Agric. at Fitchburg Dec. 2, 1873*). Boston, 1874.
Clark, W. S. "Observations on the Phenomena of Plant Life." *22d Ann. Rep. Mass. State Board of Agric.*, Boston, 1875.

laid the foundation for our scientific knowledge of the bleeding in these trees. Not until 1903, after 28 years, did the next important contribution to the problem appear. This was the bulletin from the Vermont Experiment Station,[1] and here in one hundred and forty-one pages, are extensive records of experiments and observations of the most painstaking sort, representing the work of several men during a number of sugar seasons. It is the latest and most important contribution yet made to our knowledge of the subject. The last thirty pages of this bulletin are devoted exclusively to tables recording the results of typical experiments and determinations along the various lines of research.

In the succeeding pages I shall first attempt to present in condensed form the main facts connected with maple-sap flow as determined by these investigators and then turn to a consideration of the various theories in detail. In this review my own observations are added only when they are at variance with the others.

Both Clark and the Vermont workers found slight suction obtaining in the maple tree all through the growing season. This negative pressure, averaging 2.25 kg. per sq. in. fluctuated somewhat during the season, and to a slighter extent it also showed a daily periodicity. The latter, however, was not marked. Suction continued in most cases throughout midwinter until February or March. Under certain weather conditions, however, the suction frequently lessened until the zero point was reached and positive pressure resulted. During most of the time until March the tension of any sort was almost *nil*. Then the great oscillations which are characteristic of the sugar season, and which are closely related to the phenomena of sap flow, set in to continue until the buds began to swell. After the buds swelled, the pressure quickly disappeared. Sugar has been made from the maple, according to Clark, in all the winter and spring months from October to May, but, except in the spring, always in small quantities. The flow is said to be better in October and November than later, and rarely occurs in December, January, and early February except on very warm days. During the warm December of 1905 on several

[1] Jones, C. H., Edson, A. W., Morse, W. J. "The Maple Sap Flow." *Vermont Agric. Exp. Sta.*, bull. 103, Dec. 1903.

bright mornings following cold nights, sap flowed in considerable quantity from the stubs where branches had been pruned from maple shade trees on the Cornell campus. In the daily papers were reports of sugar having been made during that same month.

The best sap days are those in which a bright sunny morning with rising temperature follows a frosty night. The flow is greatest early in the morning, decreases gradually as the day advances, and ceases altogether during cold nights. It is not a daily periodicity, however, since on many days no sap flows, while again the flow may continue all night. It seems necessary that the rising temperature should cross the 0° C. line in order that there should be a good "run" of sap. If the temperature remains for several days above this point or for several days below it, the flow will rapidly diminish, and in from 24 to 36 hours cease altogether. The trees will then "dry up" and have to be retapped, even though the temperature fluctuates considerably. Hence comes the popular belief that the roots must freeze at night in order to obtain a good "run" the following day. Depending upon the weather, therefore, the sap flow is usually broken up into periods known as "runs." The swelling of the leaf-buds marks the end of the flow, or "season." If the day be too bright after the frosty night, the flow is apt to start briskly and soon lessen or cease, or if the wind be high the flow is soon checked. If the sky be overcast and the air has warmed slightly, a satisfactory run is likely to ensue. Alternate freezing and thawing,— moderately warm days preceded by freezing nights,— are the ideal meteorological conditions which promote the flow. Other things being equal, the flow is usually greater on southern exposures, since there the temperature extremes are greater.

A manometer attached to a bleeding maple tree shows that a considerable pressure exists within the tissues of the wood. It is this pressure which causes the outflow of sap, and which is the primary phenomenon to be considered. During the best sap days the pressure may rise as high as 6.5 to 10 kg. per sq. in., but is usually less. The pressure is highest on warm sunny mornings after a frosty night, and rises very rapidly after the first sunlight strikes the tree, so that on ordinary bright sap days it has reached its maximum at nine or ten o'clock. After that it gradually decreases

toward nightfall. The time of highest pressure does not therefore coincide with that of highest temperature, but often precedes the latter by several hours. The maximum pressure on a good day usually occurs about one and one half hours after commencing in the early morning. If the following night is also cold, then all through the night a moderate suction will obtain again, to be followed by a similar abrupt rise the following morning. In one case, Clark read on the manometer at 6 A. M. a suction sufficient to raise a column of water 7.89 meters high, while as soon as the sun shone upon the tree the mercury suddenly began to rise so that at 8.15 A. M. the pressure outward was enough to sustain a column of water 5.63 meters in height, a change represented by more than 13.5 meters of water. On another morning the change was still greater representing 14.45 meters of water. If the night remains warm preceding a thaw, the fall of pressure will be much less rapid, and a moderate pressure may continue all through the night gradually vanishing during the following day. After several days of thaw, suction may obtain most, if not all of the time. If the temperature remains below freezing, suction may exist for several days until the weather warms. There is much to indicate that the normal condition in the maple at this period is one of suction.

A rise of only a few degrees will often cause very great pressure if the rise passes the zero point Centigrade. On the other hand there may be considerable fluctuation in temperature without great fluctuation in tension. This happens when the temperature does not cross the zero line. The pressure fluctuations are greatest early in the season. During the day, pressure forces into the tap-hole all the sap located in the adjacent tissue. The suction which ensues on freezing nights possibly draws more sap into these tissues, and this in turn is forced out when the tree warms up again. The entrance of air is hindered by the impermeability of the membranes.

It was found in Vermont that trees so placed that the morning sun shone on the top first, showed pressure there before in the lower trunk. On a certain day when there were alternate periods of bright sun and clouds, the gauges fluctuated very markedly. Two pressure gauges were placed at a distance of twenty feet

(6 meters) from each other on an eighteen-meter tree, one being near the ground. As a general rule the lower gauge responded first, held its pressure longest, and fluctuated more. It showed more pressure during the day and more suction at night. The higher up the gauge, other things being equal, the less the pressure. Sap conditions began first in the twigs and external layers of the wood, gradually passed to the deeper tissues and lower parts, ceasing again in the same order. Clark, on the other hand, laid emphasis on the fact that the greatest suction as well as the greatest pressure was exhibited by the gauge at the top of the tree, but his tables show that this was very unusual. In general, his upper gauge registered much below the lower and fluctuated no more than did the latter. In one case Clark found that on the 19th of April the upper gauge showed little or no pressure while the lower one still indicated a pressure of about seven kilograms. In good seasons and good sap-spells the pressure directed downward in the trunk exceeds that directed upward. Later in the season the reverse may be true. Both pressure and suction are greater in the outer than in the inner tissues until late in the season. The outer tissues respond more quickly to temperature changes, and the pressure changes here precede those in the inner wood (hole 13 cm. deep in a tree 60 cm. in diameter) by about one hour. One depth might show pressure or suction while the other showed the reverse.

Pressure is not readily transmitted radially, in fact the transmission in this direction is very slight indeed. The lateral transmission of pressure is also very slight, not much more than three millimeters, but diagonally it is transmitted quite readily. Two years' trial in Vermont showed that a 4.5 kg. pressure under some conditions is transmitted through 244 cm. of distance. Smaller pressures are not transmitted so far. It seems probable that the pressure traverses the tissue entirely by means of the tracheæ. If two tap-holes are made, one in a vertical line above the other, and either one is opened, the fall of pressure in the other is abrupt at first but after a short time ceases, and is proportional to the distance between the holes. The remaining pressure represents the resistance of the intervening tissue to the transmission of pressure. In one case a hole bored 122 cm. above a gauge in-

dicating 6.8 kg. pressure caused a drop of 3.2 kg. before a stop-cock could be inserted.

The sap flow varies in quantity with the pressure, so that a separate discussion of its characteristics is scarcely necessary. Some points, however, may be noted. On good sap days the quantity is often great, being as much sometimes as 12 liters in 10 hours. In some exceptional cases a flow of 20 liters per day has been recorded. Usually the flow is much less, 10 to 12 liters a day being an average flow for a moderately good sap day. According to the Vermont *Bulletin* it seems probable that a high registered pressure is not absolutely necessary to a good flow of sap, but that less pressure with longer duration will give equally good results. The rate of flow seems to depend also upon the amount of sap present in the wood around the tap-hole as well as upon the pressure behind it.

In general the flow is greatest near the ground. Clark inserted a spout at the usual height into a healthy maple which had never been tapped, and fifteen meters above this another spout was set into the trunk where it was 13 cm. in diameter. In addition, a limb 10.6 meters from the ground was also cut off where it was 2.5 cm. in diameter. In several hours the lower spout had bled 2.7 kg. of sap, the limb 56.7 gm., and the upper spout not a drop. Similar experiments with other trees gave like results. Both Clark and the Vermont workers found the down flow, as well as the down pressure, greater especially at the ordinary height of tapping. At both places, too, it was found that if an incision is made into a tree the sap will flow from the upper side of the cut and not from the lower unless late in the season. In late spring the flow is usually from both surfaces. In other words the flow is down from above in the maple, not up from the roots. Clark found that a severed tree would bleed profusely from the cut surface while the stump remained nearly dry. In Vermont it was found that in many cases severed twigs that started to bleed very early in the season frequently ceased before the flow from the tap-hole diminished very much. Lithium chloride inserted in the tap-hole showed that at times, at least, sap under pressure moves in the vicinity of the outlet hole at the rate of from 5 to 15 cm. per minute.

Clark found that pressure from the root during the sugar season was never more than very slight. Usually there was suction in the root throughout this period. At the Vermont Station the results were similar, the suction in one case being as much as 2.7 kg. There was a very slight fluctuation, however, between day and night as in nearly all roots. In no case was there a flow of sap from the root until late in April at the time when other trees bleed from the root. The root therefore as a source of bleeding in the maple is out of the question.

The sap of the maple is composed mainly of water with a few substances in solution. Of these, cane sugar is the most important, being present in from 1 to 5 % concentration. At first the sap is a water-clear, slightly sweet fluid, but as the season progresses the flow tends to lessen and the sap is apt to thicken and become cloudy or even somewhat slimy at times. Besides sugar there are usually small quantities of proteids, of mineral matter, more especially of lime and potash, and of acids mainly malic. Traces of reducing sugars are sometimes found, usually toward the last of the season. The sap from a tap-hole at ordinary height is considerably richer in sugar than the sap from the root, and also richer than that from taps higher up in the tree. The percent of sugar is also greater in sap from near the surface of a tree trunk than from deeper in the wood. There is some reason to believe that the actual distribution of stored material during the winter (starch and sugar) follows these conditions closely with less stored starch in the root than above ground, and less in the top than in the trunk, but accurate determinations have not been made. In Vermont it was found that at the beginning of the season sixty percent of the sugar came down from above. At the close of the season only about 39% came from the same source. There seemed to be a slight diurnal fluctuation in the percent of sugar, it being slightly greater toward nightfall.

The water content of the wood during the bleeding season varies from 30% to 55%. After the leaves come out it falls to from 19 to 30%. The Vermont workers found the relative amount for root, trunk, branch, and twig to be 29, 30, 34, and 37 respectively, but variations were so wide that the value of the series of averages is open to question.

The gas content of maple wood was found by the Vermont workers to be about 24% of the volume of the wood. This gas consists largely of oxygen, carbon dioxide, and nitrogen, which are either produced by metabolism or have passed in from the air.

During the late winter of 1904 I made a number of observations concerning the disposition of the gas in the wood of a number of trees, and the results may here be added. Sections were made with a razor either under water or under oil, and mounted in the medium in which cut. Looking quickly through the microscope before changes could occur, the disposition of the bubbles of gas could be quite readily ascertained. It was found that in the maples the vessels contained relatively little gas, sometimes appearing saturated with sap, while the wood fibers usually contained a large quantity of gas. In some cases the latter were nearly filled with gas, in others only a part of them filled, and in a few specimens of sugar maple I could find no gas in any part of the section. Nyssa and Cladrastis showed little gas in the vessels during the bleeding season, and little in the fibers. Juglans showed little in the very large vessels while the fibers seemed always to be filled with gas. The other trees examined showed more gas than sap in the vessels.

The following table gives the results in detail:—

a. Sectioned under water, and under oil

Acer pseudoplatanus. Considerable gas in vessels especially near cortex; gas in wood fibers.

Acer saccharum. No gas in inner vessels, possibly a bubble in outer; gas in fibers. Bled in room.

Acer saccharinum. No gas could be found in vessels of this specimen; gas in fibers. Branch bled in room.

Acer platanoides. No gas found in vessels of this specimen; plenty in fibers.

Acer tartaricum. Gas in vessels near bark, elsewhere none found; gas in fibers. Branch became damp in room and bled a few drops if heated on radiator.

Acer insigne. Rarely a bubble in vessels; gas in fibers. Branch bled a little in room, more on radiator.

Acer campestre. Considerable gas in vessels; gas in fibers. Became damp only on radiator.

Juglans cinerea. Little gas in vessels, but fibers filled with gas. Branches bled on radiator.

Nyssa sylvatica. Wood quite highly saturated; little gas in either vessels or fibers. Bled on radiator.

Cladrastis lutea. Same as Nyssa. Bled on radiator.

b. Sectioned under oil

Salix fragilis. Large quantity of gas in vessels and fibers. Not even damp on radiator.

Catalpa speciosa. Same as Salix.

Populus dilatata. Vessels almost full of gas. Not damp on radiator.

Ulmus americana. Same as Salix.

Fraxinus americana. Full of gas; could blow through a piece several centimeters long. Not damp on radiator.

Vitis vulpina. Full of gas. Could blow through. Not damp on radiator.

Prunus virginiana. Large quantity of gas in vessels. Not damp on radiator.

Quercus alba. Much gas. Could blow through. Did not become moist.

Regarding tree temperatures, it was found that in holes 8 cm. deep they fluctuated less than air temperatures. According to the Vermont *Bulletin* slight variations in outside temperature caused little or no variation within the tree, which on many days did not show a range of 2° C. Considerable variation in external temperature, however, was followed in due time by corresponding, though less marked, internal fluctuation. Temperatures of –3° C. and –2.5° C. were the lowest recorded during the sugar season. Thermometers placed in 2.5 cm. deep holes on the north and south side of a tree showed during the winter a lower registration on the north side at all times except one day when the south wind was blowing.

THE GAS-EXPANSION THEORY

About twenty-five percent of the volume of a maple tree is occupied by gas during the sugar season (*Vermont Bull.*). The presence of so much gas in the wood, together with its ease of detection and its known expansive qualities, early led the attention

of physiologists to this substance as a source of pressure, and until recently it has seemed to many a very probable explanation.

In 1767, Du Hamel [1] and Dalibard noticed that saturated wood became lighter when heated in hot water because of the loss of a portion of the contained fluid, and regained nearly its original weight when cooled, because of reabsorption. This was true except when the water in the wood froze, in which case the wood became again lighter in proportion to the frost.

Hartig,[2] in 1853, experimented with normal living wood using shoots of poplar, birch, etc. He found that, if these were taken before sap flow had normally begun and warmed over a lamp or in the hand, a small amount of sap would appear on the lower surface. If the temperature was near that at which sap flow normally appeared and the twig was normal, the excretion would occur to a slight extent simply by the application of the finger to the bark.

In 1860 appeared the exhaustive paper of Sachs [3] who was the first to put the gas-expansion theory on a firm scientific basis. A cylindrical stick of *Rhamnus frangula* 20 cm. long and 1.5 cm. thick, after having lain for 4 weeks in water of from 4° to 8° R. was treated and weighed as follows:—

6	hrs.	in	water	at	20°	R.	weighed	51.4	gms.	Water inside 28.6
16	"	"	"	"	3°	"	52.5	"	"	" 29.7
1	"	"	"	"	30°	"	51.4	"	"	" 28.6
2	"	"	"	"	25°	"	51.7	"	"	" 28.9
1	"	"	"	"	40°	"	51.2	"	"	" 28.4
1	"	"	"	"	2°	"	54.1	"	"	" 31.3
16	"	"	"	"	4°	"	54.2	"	"	" 31.4
1	"	"	"	"	30°	"	52.6	"	"	" 29.8
2	"	"	"	"	4°	"	54.3	"	"	" 31.5

Although, as seen from weights No. 2 and No. 7 which are at nearly the same temperature, there was a progressive increase in

[1] Du Hamel. *Du transport, de la conservation et de la force des bois.* Paris, 1767.

[2] Hartig, Th. "Ueber die endosmotischen Eigenschaften der Pflanzenhäute." *Bot. Zeit.*, vol. 11, p. 313, 1853.

[3] Sachs, J. "Quellungserscheinungen an Hölzern." *Bot. Zeit.*, vol. 18, p. 253, 1860.

weight independent of the experiment, still the abrupt change between Nos. 1 and 2, 2 and 3, 5 and 6, 8 and 9 shows very well the increase in weight when cooled and a corresponding decrease when warmed.

Similar results were obtained whether or not the wood was completely saturated, although all of Sach's experiments seem to have been with material rather near the point of saturation.

In the above experiment the weight of the twig dry was 22.8 gms. which subtracted each time gave the figures in the last column as the amount of water in the twig at each weighing. It will be seen that between 4° and 30° there was a loss of 1.6 gms. of water from the 31.4 gms., which would equal a loss of 5.09 gms. for each 100 gms. of water. Pure water, however, will expand only 1 gm. for every 100 gms. between the above temperatures.[1] Consequently water expansion alone will account for only about one fifth of the water excretion. Similar results were obtained for several other woods, including *Corylus avellana*, *Abies excelsa*, birch, beech, and oak, except that in the beech and some others the excretion was as much as seven times greater than the computed water expansion or even more. In many cases bubbles of air were extruded on warming, and none of the pieces of wood were saturated. Therefore Sachs concluded that the increased excretion of water must have been due to the expansion of gas, and this without doubt is the only true explanation of the phenomena with which he was dealing.

After recording this and several other similar experiments, Sachs felt warranted in saying that, if a rooted maple tree at a temperature of 0° R. in all its parts, is cut in two in the middle and the lower part with the roots is warmed, water will flow from the cut surface of the stump; and likewise, if the upper part with the branches is warmed, sap will flow from the other cut surface. If, on the other hand, the tree is not cut, then a pressure will arise in the trunk, which, if an incision is made, will result in a flow of sap out from both sides of the wound at the same time. Sachs considered that many phenomena were readily explicable by the assumption of water and air expansion in the wood.

[1] As given in Johnson's *Encyclopedia*, I find the expansion of water would be only 0.425 gms. for each 100 gms. between 4° and 30°; therefore less than the amount stated here by Sachs.

Sachs says: "If we assume that a stem and root has reached an even temperature between 0° and 4° R, and then suddenly a marked warming of the air occurs, at first only the crown and the stem are warmed, the thinnest twigs first of all; a part of their water is forced back into the thicker twigs, these in turn are warmed and a portion of their water is forced back into the cold trunk, which is warmed most slowly. Even this at length becomes warm and soon water is forced into the root. If now after the roots had become warm the trunk and top were to become cold through a sudden fall of temperature in the air, then a flow would occur from the roots toward the stem and from the stem toward the branches and so on." He was not sure whether this was the sole factor in the sap flow of the maple, birch, etc., in winter.[1]

But is the gas-expansion theory really capable of accounting for the *pressure* observed in the maple tree during the sugar season? In the Vermont report, a pressure of 24 lbs. (10.8 kg.) per sq. inch was given in one instance, while pressures of 10 to 15 lbs. (4.5 to 6.8 kg.) were frequent. The change in external temperature was in these cases about 5° to 8° C., which would mean a change of perhaps 3° to 4° within the tree; or, if the sun shone directly upon the tree, perhaps there would be a rise of from 5° to 10°, especially in the outer wood and twigs. Gas pressure increases at the rate of $\frac{1}{273}$ for each degree of rise in temperature. A 6.8 kg. pressure (atmospheric pressure per sq. inch) would therefore equal 6.8 $\frac{6.8}{273}$ kg. with a rise of one degree. A rise of from 5 to 10 degrees, as here supposed, would increase the pressure only from $\frac{34}{273}$ kg. to $\frac{68}{273}$ kg., a very small amount compared with the 4.5 to 9 kg. pressure actually obtained. The Vermont people are justified, therefore, in asserting that gas expansion cannot possibly account for the pressure observed in the sugar maple.

[1] For concise statement see his *Vorlesungen über Pflanzenphysiologie*, p. 245 (ed. 2). Sachs failed to distinguish between maple and birch in regard to the nature of flow. It may be also of interest to note that Sachs' conclusions were at once sustained by Hofmeister who also brought out additional evidence to their support (Hofmeister, W., "Ueber Spannung, Ausflussmenge, und Ausflussgeschwindigkeit von Säften lebender Pflanzer," *Flora*, vol. 45, p. 97, 1862).

Is the gas-expansion theory capable of accounting for the *flow* from the maple? A sap flow as high as 20 liters a day has been recorded in some instances, but under ordinary conditions the flow rarely exceeds 10 liters. If we take a tree 5 dm. in diameter and 20 meters high, and assume that the branches if pressed together in an erect position would approximately complete a cylinder with a diameter of the lower trunk and a height of the tree, we find that the volume of the tree would be approximately 3.927 cu. m. As given by the Vermont *Bulletin*, about 25% of this volume is gas or about 981,745 cc. This would expand for every degree 3596.1 cc. For a rise of from 5 to 10 degrees the expansion would be from 17,980.5 cc. to 35,961.0 cc. If we were justified in assuming the transmission of pressure without friction from all parts of the tree then this gas expansion would easily cover the ordinary 10,000 cc. flow, and even the maximum of 20,000 cc. But we are not justified in such an assumption. Resistance within the tree is great, and pressure, according to the Vermont studies, is not transmitted more than eight feet either way from the tap-hole. Therefore in such a section of the above trunk 16 ft. long (487.5 cm.) and hence containing 239,300 cc. of gas, a rise of one degree would cause an expansion of 876.5 cc. or 8765 cc. for 10 degrees. This would barely account for the ordinary flow of 10,000 cc. It is not true, however, that the whole of the water, even in such a section of the trunk, is in frictionless connection with the tap-hole. Water travels with great difficulty transversely from one annual ring to another, so that the outer layers only would probably furnish the main quantity of the sap. In such case the gas expansion of these layers would probably be only from $\frac{1}{5}$ to $\frac{1}{4}$ of the whole amount for the above section of trunk, and would scarcely account for even the smaller daily flows.

Moreover, the gas, as shown above, is at this season mostly, if not entirely, confined in the wood fibers. Gases diffuse through moistened cell walls only with difficulty so that a heavy pressure and considerable time would be required before the diffusion could be of much magnitude. In answer to this objection it might be claimed that if the wood fiber, instead of containing air alone, were partly filled with water, as is frequently true, then the expansion of the gas might press the liquid out with much greater

ease than it could pass out itself. However, the resistance in any case would be so great that to conceive of even a fourth of the total expansion being transmitted to the single small tap-hole is very difficult. Then, too, if the fibers are nearly filled with gas as seems true in many cases, early in the season at least, the expansion could be but slight before the limits of the cell cavity would be reached. As there would be no more sap to be forced from the cell and as the passage of the gas is difficult, the pressure at the tap-hole would necessarily cease altogether.

The gas-expansion theory cannot account for the pressures obtained, and can account for the volume of flow only by assuming very improbable conditions. It seems to be really out of the question. Sachs' interpretations were doubtless correct for the phenomena investigated, but the conditions in the maple tree are not of the same nature as those in the blocks of wood used in his experiments.

The Water-expansion Theory

One of the earliest as well as one of the most general of the beliefs regarding the cause of pressure in maple has referred it to the expansion of the sap itself as the temperature rose on a good sap morning. In presenting the facts favorable to such an interpretation it is important to note first that in maple during the flowing season the vessels are practically full of sap, while the gas is mostly localized in the wood fibers. It seems fair to suppose that the water can be forced from the vessels into the wood fibers only with some difficulty. Sachs showed that considerable pressure was required to force water through wood in a radial direction, and the Vermont experiments show that little pressure is transmitted laterally. Therefore if the temperature rises quickly in the morning the expanding water may be prevented from flowing at once into the fibers. Now if water is held under confinement free or nearly so from air bubbles, as is here the case, very slight expansion could cause a pressure of very great intensity for a short time. When later the water had penetrated the wood fibers, this pressure would rapidly fall just as it actually does fall in the maple tree. The maximum pressure in the maple occurs one hour or one

and one half hours after pressure begins in the morning. From this time on pressure falls gradually to the zero point. The highest pressure occurs, therefore, several hours before the time of maximum air temperature for the day, and the maximum temperature within the tree would be still later. Still the most abrupt rise is no doubt early in the morning when the sunlight first falls upon the tree, while the subsequent daily rise must be much more gradual. It might, therefore, be inferred that later in the day the percolation of sap into the fibers is sufficiently rapid to offset the expansion after the first abrupt rise.

When the temperature again falls below the freezing point, water would be drawn back into the vessels from the fibers and from more distant parts of the tree whither it had been forced. In many cases, as seen in the Vermont *Bulletin*, suction is greatest at first, but gradually decreases if the cold persists for some time. Suction during cold nights might be due either to the presence of a normal two or three pound suction in the tree at this season, or to the difficulty which the fluid that had passed into the wood fiber encountered in going back through the walls. When the temperature remains high, for a long time little pressure occurs though the fluctuations in temperature may be great. Only a previously low temperature insures a good run when the mercury again rises, and it is better if the cold endures for several days. A cause of this might be that at the high temperature, air creeps into the vessels from the expanded gas in the various tissues so that fluctuations are no longer transmitted. During the continued cold the air would pass back to the older cells thus leaving once more a solid column of water.

The objection that the sap occupies its least volume at 4 degrees and therefore at a temperature above that at which pressure begins, is invalid because only pure water behaves thus. With concentration of solution this density point falls much more rapidly than the freezing point, becomes less marked, and soon becomes identical with the freezing point so that with comparatively slight concentration it would either have disappeared entirely or at least have fallen to 0° C. when it could no longer be used as an objection.

It is possible, therefore, to explain the extreme pressure and many fluctuations peculiar to the maple by this theory, but it has

one very weak point. This is the assumed high impermeability of the fiber walls. Although it is probably impossible to force water through many such walls with the pressure observed, still we are scarcely justified in assuming that one or two walls only separating the vessels from the adjacent fibers would be so highly impermeable. This seems improbable.

To determine whether this theory will account for the volume of flow a few computations must be made. In the Vermont *Bulletin* the trunk of a certain tree was computed to contain 1220.5 lbs. (553,609.6 cc.) of water (p. 62). The coëfficient of expansion of water between 4° and 8° C. is 0.000,118 for the whole 4 degrees, which would give an increase in volume of 65.3 cc. for the whole amount. A rise from 8° to 15° C. with a coëfficient of 0.000,729 would give an additional 403.5 cc. Since tree temperatures vary only a few degrees the expansion in any case would be only a very small fraction of the whole flow. For a tree 20 meters high and 5 dm. in diameter, the volume would be 3.927 cu. m., provided that the branches if pressed together would approximately fill out the trunk cylinder to the total height of the tree. If a cubic foot of dry maple wood weighs 43.08 lbs. the dry tree would weigh 2,709,895 gms., 45% of the tree is water, and 55% is wood; therefore, the weight of the water would be 2,217,332 gms. The expansion from 4° to 8° C. would be 261.7 cc. If it were possible to believe that the water of the whole tree could flow to the tap-hole without resistance, the flow would be still only one fourth to one half of the actual daily flow. Since, however, it has been shown that pressure is transmitted only about eight feet each way from the tap-hole, the volume of water which expansion might cause to flow to the tap-hole would be only a fraction of the whole. If water passes into the wood fibers to any extent the flow due to expansion would be still less, only about $\frac{1}{12}$ to $\frac{1}{6}$ of the whole flow.

The wood of the majority of trees is structurally so constituted as to render the passage of water difficult radially from one annual ring to another, while at the same time there may be fairly good communication laterally owing to the bordered pits (in the Coniferæ) and the anastomosis of vessels in the broad-leaf trees. It is very probable, therefore, that not the whole 16-foot (4.8 meters)

section of the trunk would be tributary to the tap-hole, but only the few outer layers. If this be true, the flow to be expected from this source would be an extremely small fraction of the whole flow, not more than $\frac{1}{36}$ to $\frac{1}{18}$. It is obvious, therefore, that sap expansion cannot account for the flow in the maple.

Moreover, it is also not easy to see why air should pass back into the wood fibers on cooling below 0° C. at a time when there is actual suction in the vessels. Even if this were possible the theory cannot account for the flow, and can account for the pressure only by supposing the walls of the wood fibers impervious to water to an extent beyond the range of probability. The water-expansion theory must therefore be considered almost, if not quite, out of the question.

THE WOOD-EXPANSION THEORY

There is still another possible source of pressure due to heat expansion, namely, the expansion of the wood itself. Wood expands, as well as swells, more in transverse than in longitudinal direction. The coëfficient of expansion as determined by Villari [1] for dry maple wood is 0.000,006,38 in longitudinal direction, and 0.000,048,4 parallel with the radius. The coëfficient for wet wood is not recorded, but it must be considerably greater.

Let us suppose that the rising sun falls abruptly upon the tree or that the air temperature itself rises rapidly; then the outer layer of wood will be warmed much more rapidly than the inner, and probably the rise will be several degrees in the outermost layers. These outer layers will tend to expand, but being firmly united with the inner, such expansion is possible only to the extent of the elasticity of the wood. The result will be, therefore, a pressure among the elements composing the outer layers. The vessels of maple wood are quite large and surrounded by fibers. Since the latter contain the bulk of the wall-substance, they, in expanding, would tend to press upon the large cavities, the vessels. Since

[1] Villari, L. "Experimental-Untersuchungen über einige Eigenschaften des mit seinen Fasern parallel oder transversal durchschnittenen Holzes." *Pogg. Ann. d. Physik u. Chemie,* vol. 133, p. 400, 1868.

the walls of the vessels are not so thick as those of the fibers, it is very likely that the large tubes would become to a slight extent collapsed. If they were completely filled with sap, the pressure would be transmitted directly to the pressure gauge. Later in the day, the temperature having penetrated to the inner layers of the tree, the pressure would disappear. Such a theory could also account for the very slight pressure observed in twigs which have a small diameter and are therefore quickly heated throughout.

Again, from another standpoint,[1] it is known that wood expands more across grain than longitudinally. Probably, like the swelling of wood cells, this is dependent upon the micellar structure of the walls themselves. As in the case of swelling therefore, it may be that the wood is free to expand tangentially, but is retarded radially by the massive pith-rays, the cells of which lie upon their side so to speak, and therefore expand less in the radial direction. The wood may in this way, independent of the contrast between inner and outer temperature develop an internal pressure, which would tend to compress the vessels as in the previous case. Pressure produced by this method, however, would not tend to disappear with the penetration of the heat.

As in the water-expansion theory, here, too, the same relation must be supposed to exist between the wood fibers and the vessels, and the same impenetrability of the walls must be assumed. Consequently the objection must again be brought forward to assuming such a high degree of impermeability. The expansion of wood is even less than that of water and hence a still higher impermeability must be assumed. Granted this impermeability, however, an almost unlimited pressure could be theoretically obtained.

Suction could be accounted for, as in the water-expansion theory, either by supposing a normal two or three pound suction in the tree, or by supposing that some fluid had passed into the wood fibers and was retarded in its return.

The occurrence of maximum pressure so early in the day could be accounted for under the first method of pressure-origin by assuming that after a short time the temperature in the outer and inner layers had equalized to a large extent; and under the other

[1] Roth, F. "Timber." *U. S. Dept. Agric., Dept. Forestry*, bull. 10, p. 32.

method by assuming that after the first abrupt expansion the sap flowed off through the tissues to the wood fibers, or to more distant parts of the tree faster than expansion took place.

Let us take the same case cited under the water-expansion theory of a maple tree 20 meters high and 5 dm. in diameter at the base, and a volume approximately 3.926,98 cu. m. as determined above. The radial coëfficient of expansion for dry maple wood is 0.000,048,4; if wet it would be greater, suppose 0.000,088,4. In tangential direction it would probably be greater still owing to the absence of pith-rays, say 0.000,15 or an average coëfficient of 0.000,119,2. The radius is 0.25 m., and for one degree of rise it would become 0.250,029,8 m.; the area would be 0.196,396 sq. m., and assuming that the length remains the same, the volume would be 3.927,92 cu. m., an increase of 940 cc. for one degree, or 3660 cc. for four degrees. This is only about 3.6 liters to be compared with the actual flow often of 10 or more liters. Under the most favorable conditions, presupposing the transmission of pressure from the most distant parts of the tree, and the equal penetration of heat, the flow would be only a fraction of the total flow on many days. If the pressure is transmitted only eight feet each way the flow would be slight indeed, and if produced only in the outer layers, as it would be necessary to suppose if we consider the pressure due to contrast between inner and outer temperatures, the flow would be insignificant.

In order that the pressure should become evident at all from such a source an almost absolute impermeability of the fiber walls must be assumed, otherwise the very insignificant amount of expanded water would in a very short time pass through and pressure would soon cease. This theory, therefore, fails to account for the volume of sap flow; and pressure can be accounted for only by assuming the almost absolute impermeability of the walls and saturation of the vessels, the former of which at least, is very improbable.

COMBINATION OF GAS- AND WATER-EXPANSION THEORIES

It has been shown that the expansion of the gas cannot account for the pressure, and can account for the volume of flow only when the resistance within the tree is reduced to a point considerably

below what we should expect. Supposing, however, that it is able to account for the flow, is there any way of combining this with the water expansion so that the water expansion will account for the pressure and the gas expansion for the flow?

Early in the sap season the wood fibers appear filled with gas while the vessels are nearly or quite saturated with sap. The sunlight falling upon the tree in the early morning would rather abruptly warm the outer layers several degrees. Provided now that the walls of the fibers are slowly permeable to water, as has already been shown to be the case to some extent, then a high pressure would be produced by the expansion of the water in the vessels. Rapid expansion would quickly diminish, however, and the slow filtration of sap into the wood fibers would at first counterbalance the remaining expansion, then finally reduce the whole pressure gradually to nearly zero. Fall in temperature late in the day would aid this. Since some of the sap has passed into the wood fibers there would be suction at first at night. This would gradually decrease as the night progresses owing to the return filtration from the wood fibers. This theory could therefore account for the fall in pressure before the maximum temperature in the outside air is reached. Since the fall of temperature is always more gradual than the rise, due to the direct rays of the sun, the suction at night would never be as great as the day pressure, and it never is. After several days of rapid fluctuation of temperature, or after a period of warm weather, gas might separate in the vessels thereby rapidly diminishing the pressure to be obtained by equal fluctuations of temperature. This fact would account for the cessation of flow during a protracted thaw. A continued period of cold, however, might cause the absorption of gas and the resaturation of the vessels.

The flow can be accounted for by this theory only by supposing the wood fibers but partly filled with gas, thus allowing expansion. The expansion of the gas within the cells as the temperature rises will gradually force sap out into the vessels. The sap will then flow from the tree if tapped until the gas expansion is completed.

The objections to this theory are several. It must assume an impermeability of the wall substance which is beyond probability. Again, the volume of water produced by expansion is only about

one liter from the whole tree. Since this is distributed over the whole tree, and the numerous vessels expose an immense surface to the wood fibers, an almost complete impermeability would be necessary to affect the pressure markedly. But the gas expansion must later be supposed to overcome this same resistance. Considering the weak pressure of the gas and its compressibility it would be impossible for more than a small fraction of the whole volume of gas expansion to be transmitted to the tap-hole. The volume of flow is only barely accounted for by the total gas expansion, hence under these conditions only a small fraction of the flow would occur. Again, if gas expansion in the fibers causes flow, the latter would rise to a maximum slightly after the air temperature. The water expansion in the vessels would tend, however, to cause maximum flow at maximum pressure. The actual maximum would be a resultant of the two, so the curve of flow would reach its maximum later than the pressure curve and fall much more slowly. This is not the case with curves prepared from tables in the Vermont report. The curves of pressure and flow are almost exactly coincident.

It seems evident therefore that this theory also must be laid aside.

COMBINATION OF WOOD-EXPANSION AND GAS THEORIES

It has been suggested that although the expansion of the wood is not sufficient to account for the total flow of sap, still, if combined with the gas expansion, the two together might account for both pressure and flow. Granting that the vessels are nearly if not quite saturated with water and that the gas is mainly within the wood fibers, both of which conditions seem to be true, then when the tree warms, the conditions would be as follows. The rapid warming of the outer layers of wood when the sun first falls upon them in the early morning would produce pressure as already outlined. With the vessels saturated, this pressure might be very great. As the day progresses the expansion of the wood goes on more slowly, and as the inner layers become warmed the outer layers are subjected to constantly decreasing strain. Meanwhile the sap would be constantly but slowly filtering through the walls

into the cavities of the wood fibers and thus compressing the gas there present. This filtration, although too slow to offset all the pressure early in the day would materially decrease it, and later overcome it altogether. But the gas has meanwhile become warmed and tends to force water back into the vessels. If the tap-hole is open, a flow due to the gas expansion would occur. Such a flow would be greatest early in the day when the wood expansion was also acting and gradually decrease but at a much slower rate than the decrease of pressure, due to the great elasticity of the gas and to the fact that the maximum volume of the gas would be at maximum temperature. The retarding effect of the slow conduction of heat would probably postpone the maximum still later. If we assume, therefore, that the expansion of gas at these temperatures is great enough to account for the volume of flow, then this theory might possibly furnish a means of accounting for the pressure and flow together.

The objections are several, and fatal to the theory. The most important objection lies in the probability that gas expansion cannot account for the flow, as outlined above under the discussion of that theory. Much less could the gas account for the flow if considerable force were required to transfer the sap through the walls of the vessels, as our present theory demands. Again, as described under the water-expansion theory, we have no good reason to assume such an almost absolute impermeability of the cell walls to water. Again, curves plotted from tables XVI and XVII of the Vermont report show that the sap-flow and pressure curves are practically parallel. The maximum pressure and maximum flow are coincident, and both decrease gradually and equally as the day advances. The maximum of each occurs usually within an hour or two after starting, and the fall begins some time before the maximum temperature of the air, much less of the tree, is reached.

This theory also must be laid aside as improbable.

THE FREEZING THEORY

Professor Clark[1] and others were inclined to believe the pressure in the maple due to the expansion caused by the freezing of the water within the tissue. "The sap is separated from the cellulose of the wood by the cold and under ordinary conditions reabsorbed. The bleeding is, therefore, a sort of leakage from the wood, but this is doubtless increased by the elastic forces of the gases in the tree which are compressed by the liberated sap, and the expansive power must be intensified by the increase in temperature which always accompanies a flow.

"This theory explains the fluctuation of the gauges, and accounts for the singular fact that the upper one shows the most pressure and the greatest variations in as much as the branches and twigs would of course be most quickly and powerfully affected by the heat of the sun and the temperature of the atmosphere. The pressure of the expanded gases in a tree in a normal condition would facilitate the reabsorption by the wood of the liberated sap. Their contraction by cold would also cause the cessation of flow from a tree which was running, and produce the remarkable phenomenon of suction exhibited by the gauges at night or during frosty weather."

That the water would be drawn from the walls, our present knowledge of the freezing process shows to be true. First, the water in the lumen would congeal, then to these crystals water of imbibition in the walls would flow. If at the start the vessels are nearly or quite saturated, then the extra water from the walls, together with the expansion of the forming ice, would very naturally cause great pressure. In this wise the walls of the vessels or other chambers containing ice would be forced apart in proportion to their elasticity so that on thawing, the water would be under great pressure until sufficient time had elapsed for it to return again to the cells and walls from which it came.

It is difficult to compute the amount of flow that could be expected from such a source of pressure, but it might be considerable depending upon the amount of elastic expansion of the tracheal

[1] Clark. *Observations on the Phenomena of Plant-life*, p. 62.

walls, and the slowness of the return of water to its original location in the walls.

The objections to this theory are very serious. Firstly, the forces of imbibition are sufficiently strong ordinarily to insure a comparatively rapid return of water to the cell walls. The return of water to the walls in thawing winter buds I have observed to take place almost immediately. Flow and pressure throughout the entire day could not be accounted for in this way. Secondly, ice does not form in wood at the temperatures obtaining during the season of flow. A tree temperature of –3° C. was the lowest obtained by the Vermont Station during this period, while on many good sap days the tree temperature at night was only –0.5° or –1° C. The overcooling point, not the true freezing point, is of importance in determining whether ice will be formed, and this is always several degrees lower than the freezing point in all plant tissue. Both are lower than the freezing point of pure water. Müller-Thurgau [1] found these temperatures for various sorts of wood as follows:—

	overcool. pt.	freez. pt.
Stem of small apple tree	–7.2° C.	
One year shoot of pear	–3.9	–0.22° C.
One year shoot of pear	–2.18	–0.25
Old wood of grape	–6.05	–2.85
Young wood of grape	–2.9	–2.1
" " " "	–3.5	–3.35
" " " "	–2.9	–2.5
Fir wood	–5.4	–0.4

The overcooling point seems to be greater in the more dense woods than in the grape probably because of the large vessels and watery sap offering little resistance to the inception of ice formation. Maple wood would be of the closer grained type. Ice formation would probably not commence before a temperature of –4° to –7° C. was reached. Dixon and Joly [2] found that ice began

[1] Müller-Thurgau. "Ueber das Gefrieren und Erfrieren der Pflanzen." *Landw. Jahrb.*, vol. 15, p. 492, 1886.

[2] Dixon and Joly. "The Path of the Transpiration Current." *Ann. Bot.*, vol. 9, p. 416, 1895.

to form in wood of Taxus at −10° or −11° C. Therefore only during the coldest nights of the sugar season could ice ever form in the wood. Some of the aberrations in the readings obtained by various investigators on very cold nights seem to be due to this cause, since it is not improbable that if ice actually does form in the vessels an increase of pressure at night rather than a decrease may be evident for a time.

Freezing, therefore, plays no important part in the phenomena under discussion.

THEORY THAT PRESSURE IS DUE TO ACTIVITY OF LIVING CELLS

Having exhausted the possibilities in which mere physical force due to expansion is the main factor, we come now to the theories in which protoplasm plays the main part.

Pressure cannot be caused by the contraction of the protoplasm with forcible ejection of the sap because of the fragile nature of the ectoplasm. Even if this were sufficiently strong no pressure could be obtained unless the exit from the contracting sack was into a reservoir unconnected with the space around the remaining surface of the sack. Otherwise the extruded sap would simply occupy the space left by the contracting protoplasm, and no increase in volume would take place. The alternative then, is for the pressure to be caused by osmotic phenomena. Pressure and flow if accounted for in this way must presuppose an exudation, under pressure, of sap from the living cells.

Exudation is known to occur in Mucor as described by Pfeffer. In Spirogyra at very low temperatures near zero C., water has been observed to appear in droplets upon the surface of the cells.[1]

Drops of water are secreted from the cells of the pulvinus in Mimosa when stimulated, and from the sensitive staminal filament of the Cynareæ. At present bleeding pressures in root and stem tissues can be accounted for in no other way. The phenomenon

[1] Pfeffer. *Pflanzenphysiologie*, ed. 2.

Greeley, A. W. "On the Analogy between the Effects of Loss of Water and Lowering of Temperature." *Amer. Journ. Physiol.*, vol. 6, p. 122, 1901.

Livingston, B. E. *The Role of Diffusion and Osmotic Pressure in Plants.* Chicago, 1903.

is, therefore, one known to occur in plant tissues and is apparently much more widespread than was formerly supposed. Research is tending to show that bleeding occurs among cells of widely different tissues, and is probably to be considered a normal and very general phenomenon in plants.[1]

The exudation can be conceived to be produced in either of two ways: either by change in permeability of the diffusion membrane allowing water to pass with less friction, or by a change in osmotic tension. In regard to the first method it may be said that although diffusion membranes are considered to be freely permeable to water they really are not quite so. A force is required to press water through such a membrane as is shown by the fact that a bladder may be filled with water and suspended in air without the water escaping immediately. It is conceivable, therefore, that a portion of the cell membrane might become quite freely permeable to the solvent while the remainder continued dense. But so far as we know the resistance to the passage of water is very slight and plays no great part in the determination of pressure in osmotically active cells. So far as our knowledge goes, osmotic pressures are the same, no matter what membranes are used, providing that the solute is of the same nature and density, and that the membrane is permeable to it in the same degree, and also permeable to water. The osmotic pressure of water has been demonstrated in connection with some artificial membranes, but was always found to be slight. So far as we know at present all pressures of any moment in connection with semipermeable membranes are produced directly or indirectly by the action of the solute, and are proportional to the quantity of the latter present.

We have remaining the alternative of a change in osmotic tension. But such an alteration in osmotic tension is not sufficient in itself. Water might be excreted from the cells by a simple change in permeability of this sort, but the production of pressure in the surrounding tissue would be impossible, for as the water passed out from the cell, the latter would decrease a like amount in volume and no pressure would ensue, simply a change of location

[1] Wieler, A. "Das Bluten der Pflanzen." *Cohn's Beiträge*, vol. 6, p. 1, 1892. See also Pfeffer, *Pflanzenphysiologie*.

of the water with reference to the membrane of the cell. To obtain pressure externally by osmotic action it is necessary to assume a *flow* of water through the cell. But if the two reservoirs of supply and excretion are confluent then there will be a flow through the cell, in at one point and out at another and back again outside to the starting point, thus forming a circle of flow; and there would be no external pressure. The reservoir of supply to the cell must be distinct from the reservoir of excretion. Pressure will then be produced in the latter reservoir while at the same time, in the former a tendency toward suction will occur.

Flow through a cell will occur as Pfeffer [1] has already shown (*a*) if the solute passes through the membrane more easily at one end than at the other. Osmotic tension will here be less and the water will be forced out by the tendency to greater pressure at the other end. Flow will be in at the side of less permeability and out at that of greater permeability. Such a condition has been demonstrated experimentally in an artificial cell by Copeland.[2] Or (*b*) a flow will occur if the solute is more concentrated at one end of the cell. Water would enter in this case at the region of greatest concentration (greatest osmotic pressure), and pass out at the region of least concentration; and would continue to flow as long as the solute remained thus distributed. The difficulty in this case would lie in the maintenance of unequal concentration of the solute within the same cell. Since diffusion would soon equalize any such irregularity it could be accomplished only by the constant production of more solute at a certain point.

If pressure is due to the unequal permeability of the membrane to solute then there must always be a secretion of solute along with the sap into the chamber showing the increased pressure. Sap in this reservoir cannot be pure water, or even nearly pure water, unless the plant possesses some means of ridding the sap of such solute after its excretion either by its immediate change to solid form or its use in metabolism. In case pressure is due to an unequal distribution of solute within the cell then no excretion

[1] Pfeffer. *Pflanzenphysiologie*, ed. 2.

[2] Copeland, E. B. "Physiological Notes II, an Artificial Endodermis Cell." *Bot. Gaz.*, vol. 29, p. 437, 1900.

of the solute into the receiving reservoir would necessarily occur. The exuded sap, in such cases, might be pure water.

That the production of comparatively great pressure is possible in either of these ways is apparent. As shown by Pfeffer's table (p. 146) a difference of one percent in concentration of sugar solution is equal to a pressure of about 0.69 atmospheres or 10.3 lbs. (4.6 kg.). Twenty pounds pressure, which is about the maximum for the maple, would be equivalent to a difference of 2 % in concentration. This is not too great to expect considering that the percent of sugar in maple sap is from 1 to 5.5 and that local concentration might be much greater for a short time before diffusion. One might reasonably expect a higher pressure.

It is very difficult to bring forward any general theoretical evidence to establish the impossibility of either the excretion of solute theory, or the unequal distribution theory. But the fact that sugar actually passes into the vessels in large quantities lends a probability almost convincing to the idea that the increased permeability allowing the sugar to escape is also the cause of the pressure.

Maple wood is diffuse-porous, the vessels being scattered rather evenly throughout the annual ring, although they are perhaps slightly more numerous in the spring wood. The vessels are large, solitary, or, more usually, two or three together and surrounded by the moderately thick-walled wood fibers. These latter form the main bulk of the woody portion. Wood parenchyma is very scarce, and is confined to a few rows of cells in the vicinity of the vessels at points where they are adjacent to the pith rays. There is some question whether this tissue is wood parenchyma since there are no cross walls as ordinarily; or whether the cells are not wood fibers like the rest but with cellulose walls. I am inclined toward the latter view since the similarity is otherwise so striking. The wood fibers are without markings but the vessels are densely pitted. Pith rays are numerous in maple and very large (Fig. 1). An estimate seems to show that they occupy about one fourth of the volume of the wood. The larger ones are from 8 to 10 cells high and from 3 to 4 cells thick, ellipsoidal in tangential section, and extend from the cortex to varying depths into the wood, some reaching to the center. The cells of the pith

rays are slightly smaller in diameter than are the wood fibers, and the walls are thick and lignified. In radial direction they are from 3 to 5 times as long as wide. Through the various walls pits extend. These are sparse on the side walls adjacent to the wood fibers, and are simply very narrow canals extending at least part way through the wall. I was not able to demonstrate that

Fig. 1.— Maple wood, tangential section. Note the massive pith rays, and the large number of wood fibers.

they passed entirely through. At any rate the communication laterally through the walls must be slight, and passage difficult. Similar narrow pits, though somewhat larger, are very abundant on the end walls, and, except possibly for a closing membrane, are very obviously continuous from one cell to another (Fig. 2).

When the pith rays are contiguous to a vessel, large bordered pits are abundant in the common wall between them. Elsewhere on the vessels, pits seem to be absent, except in the walls between the few wood parenchyma cells and the vessels. Preparations stained with hæmatoxylin showed purple in the wood only where pith

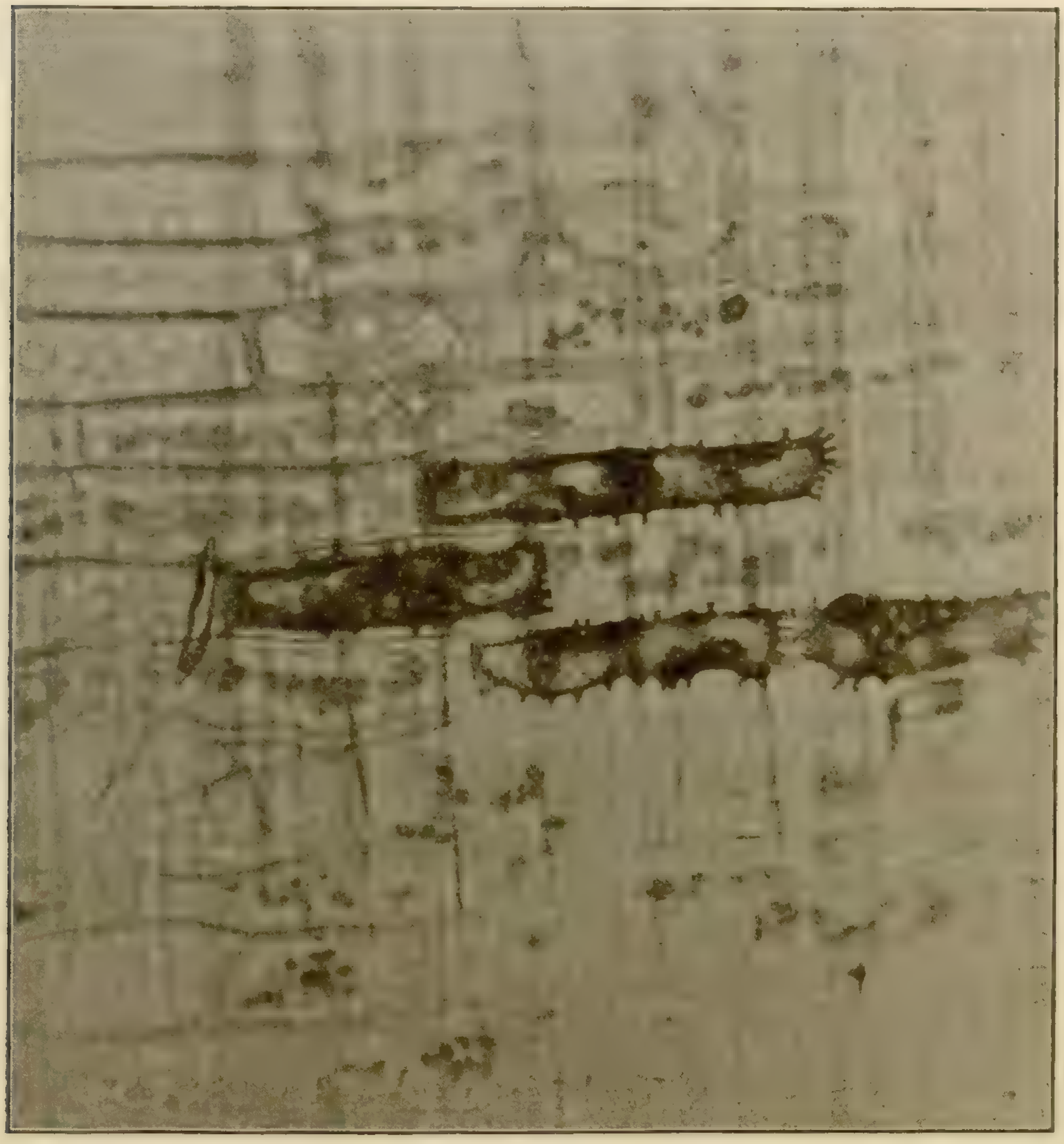

FIG. 2.— Pith ray of maple in radial view stained with iodine. The cavities of the four dark cells are filled with gas. This causes the pits to become very plainly visible. The dark bodies in the other cells are starch grains.

rays, or the sparse wood parenchyma touched the vessels. It seems probable therefore, that all the walls are lignified except just at these regions that stain, and these probably remain cellulose.

On March 25th, sections stained with iodine after the hæmatoxylin showed the pith rays well filled with starch. Starch was also present in abundance in the wood parenchyma cells about the

vessels, and in some of the wood fibers. The starch-containing fibers were mostly either adjacent to the vessels or clustered in a band at the end of each year's growth. The other wood fibers contained none at all. All of these cells with starch are living and contain protoplasm. In autumn we find the starch-containing cells of the maple packed full of this substance as in other trees. From the time cold weather commences until spring, starch is gradually converted into sugar. Fischer [1] has found this to be the case in many trees. The Vermont workers also found the starch content to decrease in early spring, and the sugar-content to increase. There is, however, no evidence to show that sugar is again reconverted into starch in late spring as Fischer states to be the case in some trees. It seems that the starch stored in the pith-ray cells and in the wood fibers described above is gradually converted into sugar as spring advances. Since there is no other source for the constantly increasing sugar content of the sap in the vessels it seems reasonably certain that this sugar escapes into the vessels from the starch cells where it is formed.

If pressure and flow are due to the living cells they must then be due to the pith-ray system, the wood-fiber system, or both, since these constitute the living part of the wood. In wood, as shown by Sachs, the only direction in which water passes with difficulty is radially. In longitudinal and tangential directions there is little obstruction to the flow. Moreover, although in the previous discussions in this paper, the fiber walls were hypothetically considered as almost impermeable to water, it seems more likely that one or even two walls intervening would retard the passage of water but little. At any rate, it is scarcely probable that a strand of starch-containing wood fibers contiguous to a vessel at one end would be more than two or three walls distant at the other end, and therefore there would be no way of obtaining for such a strand the two distinct water reservoirs necessary for the production of pressure.

In order that a homogeneous membrane should become suddenly more permeable at certain regions at a definite rising temperature

[1] Fischer, A. "Beiträge zur Physiologie der Holzgewächse." *Pringsh. Jahrb.*, vol. 22, p. 73, 1891.

only, it seems reasonable that some stimulus must be applied, and since other factors are practically constant, it seems reasonable to expect this stimulus to be the rising temperature. It is difficult to think of any other factor among the conditions obtaining in a bleeding maple tree that could give such a stimulus. But the temperature changes would reach all parts of a narrow longitudinal wood fiber at almost the same time, and the stimulus would not in that case be unequal. For these reasons it seems improbable that the wood fibers can take any great part in the production of pressure and flow.

This is not the case, however, with the pith rays. Extending radially through the wood with few lateral pits and numerous end ones, they are admirably adapted for radial conduction without much lateral loss. Only at comparatively long intervals where they touch a vessel are they connected with the surrounding wood. The radial conduction of water in any wood is very limited, and the many layers of wood fibers in this case would form an especially efficient barrier between the inner and outer wood, each layer of which could here serve as one reservoir of the system. If we suppose the ray cells more permeable to sugar at the outer or the inner ends, then conditions are all suitable for the production of pressure and flow. The penetration of early morning heat would tend to warm all of the radially elongated ray cells at the outer end before the inner. Throughout the whole period of rising temperature therefore one end of each cell would be slightly warmer than the other. It is easy to conceive of this condition acting as a stimulus to cause a similar unequal permeability in all the cells.

We may conceive of the phenomenon occurring somewhat in this way. During the winter months but little starch is converted into sugar. As spring approaches, and up to the time of vernation, the stored starch is gradually converted. In this way the sap of the living cell must become highly concentrated and the osmotic force very great. During constant temperature, however, the protoplasmic membranes are either almost equally permeable to sugar over all parts of their surface, or not permeable at all. The latter is not probable since the concentration within the cell would soon become very great.

Rising temperature, however, by warming the peripheral ends

of the cells first, acts as a stimulus and causes the ray cells to become more permeable to sugar at one end, which is the same end in every case. Since the greater pressure and sugar content is in the outer wood, it seems probable that the outer ends of the ray cells rather than the inner become more permeable, and the flow would be therefore from the heart wood toward the cortex. In an untapped tree of course there would be scarcely any flow, simply statical pressure, but sugar would pass into the vessels just the same. But the mechanism cannot be quite as simple as it seems

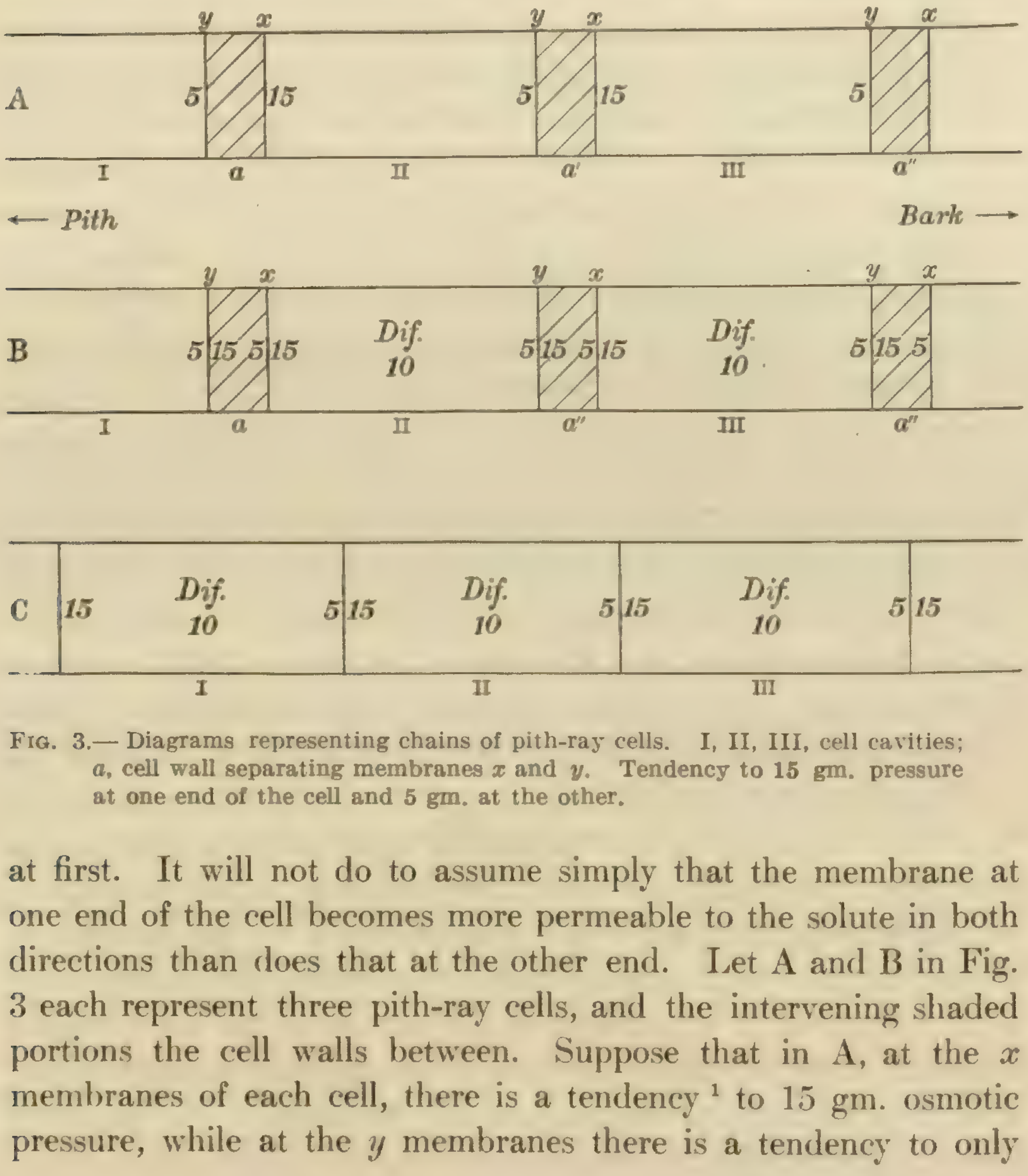

FIG. 3.— Diagrams representing chains of pith-ray cells. I, II, III, cell cavities; *a*, cell wall separating membranes *x* and *y*. Tendency to 15 gm. pressure at one end of the cell and 5 gm. at the other.

at first. It will not do to assume simply that the membrane at one end of the cell becomes more permeable to the solute in both directions than does that at the other end. Let A and B in Fig. 3 each represent three pith-ray cells, and the intervening shaded portions the cell walls between. Suppose that in A, at the *x* membranes of each cell, there is a tendency [1] to 15 gm. osmotic pressure, while at the *y* membranes there is a tendency to only

[1] The word *tendency* is here used because in all parts of a liquid the hydrostatic pressure must really be the same.

5 gms. Sufficient sugar is passing out through the y membranes to equal the difference of 10 gms. pressure. The sugar now in chamber a would tend to exert a pressure of 15 gms. toward membrane x and a pressure of 10 gms. against membrane y, which would cause a reverse pressure of 10 gms. offsetting the pressure caused by the cell. Only if the solute could be carried away as soon as excreted could this mechanism work to produce pressure, but the assumption of such freedom for the solute would necessitate a still greater freedom for the solvent, which would make the existence of two unconnected reservoirs impossible. It is obvious therefore that no pressure can be produced by this method. In order to obtain pressure it is necessary to assume unequal permeability of the membrane in the two directions. In B we may suppose each end membrane to show a tendency to 5 gm. pressure on its left-hand side and 15 gms. pressure on its right. Then water would pass from the cell to chamber a under 10 gms. pressure, and from this chamber to the next cell under 10 gms. again, and so on. This arrangement would also account for the passage of sugar from one cell to another, which could not be explained by the first method.

If, as there seems some reason to believe, the two membranes on either side of the cell wall act as one owing to the numerous plasma connections between them, then, as may be seen from C, (Fig. 3), the assumption of unequal permeability of the same membrane in opposite directions is the only one that will account for the phenomenon. It seems, therefore, that in any case we must assume not simply that the membrane at one end of the cell is more permeable than that at the other, but that each end membrane is more permeable in the direction toward the bark than toward the pith.

I see no reason why the pressure produced by the various cells should not be accumulative, that is, if we have three cells each producing a 10 gms. pressure we might expect a pressure of 30 gms. at the end of the series, or perhaps even double that if it is assumed that the cell wall forms a distinct chamber. For example, in B (Fig. 3) sap from cell I is forced into chamber a under 10 gms. pressure. Chamber a forces sap into cell II under a pressure of 10 gms. also; but, disregarding friction, cell I would have forced

water through the cavity *a* into cell II with 10 gms. pressure if *a* had contained only pure water. Is it not reasonable then that sap would be actually forced into cell II under 10 + 10 gms. pressure, and so on? If this is true then it would seem that the longer the pith ray the greater would be the peripheral pressure. Large trees would be expected to show more pressure than small ones. Unfortunately, records of pressure in trees of various sizes have not yet been made.

But it is not necessary or even probable that this is the case. The temperature each morning penetrates the wood in a wave-like manner. Only a few cells in each pith ray would be subject to the critical temperature at the same time; those farther within would be yet unstimulated, while those farther out would be recovering from the stimulation. Therefore but few cells would actually take part in the production of pressure at any one time. If this is true, the size of the tree would have little effect upon the pressure, within certain limits. I am inclined to suspect, however, that the diminished pressure in the branches and twigs may be, in the main, owing to this.

The question naturally arises why, if conditions are as here outlined, a pressure of 9 kg. in the outer wood would not necessarily be accompanied by a suction of 9 kg. in the inner wood, or indeed by 9 kg. plus the natural suction of the tree; but no such suction as this has been recorded. It may be mentioned that there seem to be no recorded accounts of search for pressure or suction at a greater depth than 10 to 13 cm. But the question may be considered from another standpoint. As stated above, the production of pressure would probably be confined to a comparatively few cells in each series. When pressure begins in the morning the active zone is near the bark, and water would be forced into a comparatively limited chamber, the contained gas would be rapidly compressed, and great pressure would be produced; but the water would be drawn from all the other layers of the trunk. The gas of all these layers would be expanded only a very slight amount, and little extra suction would be produced. Incidentally, the high pressures have all been recorded in the outer wood soon after flow began in the morning.

The rising temperature probably does not act as a constantly

increasing stimulus, but as an abrupt one. As the critical temperature is reached the mechanism of stimulation is perhaps set off all at once, so to speak, and the maximum permeability is reached very soon, and consequently the maximum pressure and flow. As the day progresses either the already converted sugar in the cell is exhausted or the membrane gradually recovers its normal condition as it recovers from the stimulus. It seems more likely that the recovery is not due to the exhaustion of sugar content because on succeeding warm days without freezing nights there is still evident considerable fluctuation with temperature showing that some sugar is still there. Then again, if the membrane remained unequally permeable, the small amount of sugar conversion that does constantly occur would tend to maintain a constant though slight pressure until by a fall to 0° C. the membrane became again equally permeable; but instead suction usually soon occurs. It seems much more reasonable that after the abrupt stimulation the protoplasm should soon gradually recover its original condition. The slight fluctuation in pressure that occurs each morning even during a thaw period is probably due either to a recurring but slighter degree of difference in permeability, or to an abrupt increase in sugar production induced by the rising temperature. Since abrupt fluctuation in sugar production sufficient to cause pressure is improbable, the former hypothesis seems the more reasonable.

There is no reason to believe the conversion of sugar to be otherwise than normal, that is, gradual and constantly progressive, less rapid when the temperature is low and more rapid when higher according to the normal action of enzymes. I see no reason to assume that at 0° C. enzyme activity is abruptly stimulated, thereby converting a large quantity of starch into sugar abruptly at one end of the cell, and thus causing pressure through the unequal distribution of the solute. It seems to me more probable that at a low temperature the membrane is comparatively and almost uniformly impermeable over its entire surface. Osmotic pressure is therefore high and the cells are very turgid. A rise of temperature to the critical point now causes the abrupt stimulating shock, sugar passes out at the peripheral ends of the cells, and both pressure and flow become great toward the outer wood. After

the first shock the cell begins to recover until the permeability is again equalized and pressure and flow cease. When the permeability is equalized at a high temperature, as well as at a low one, suction ensues. Hence the suction so often observed during the latter part of the thaw period. This suction may be partly due to the pressure having expelled part of the sap from the outer layers down toward the root or up toward the branches. Then after the restoration of equal permeability the tendency to equalize with the suction of the inner wood would tend to cause some suction in the outer trunk. The suction during cold nights may be partly due to the inner ends of the pith-ray cells being warmer than the outer thereby causing unequal permeability and consequent pressure in the reverse direction. But I believe that the wood of maple is normally under suction at this period, as is that of so many other trees, and that the return to suction either at a high or low temperature is merely a return to the normal. There is probably always some increase in permeability whenever one end of the cell is warmer than the other, hence pressure does not drop to zero until after the temperature has become equalized throughout the trunk each day; and on succeeding days, even if there has been no frost, the morning rise of temperature causes some pressure because of the same unequal warming. It seems reasonable to suppose that some sugar passes into the vessels at all times during the period of starch conversion, otherwise the concentration in the cells would become very great. The passage is probably less at low temperatures and greater at high temperatures. The warmer end of the cell is therefore always the one toward which flow is directed. Maple probably differs from other trees having starch stored in the pith rays mainly in (*a*) the sensitiveness to temperature causing marked unequal permeability at the two ends of the cell and (*b*) the spasmodic effect of this stimulus when the temperature is rising past a certain critical point.

The protoplasm of all sugar maple trees is probably not equally sensitive. For instance, for a number of years I have observed a tree which flowed comparatively little sap although this was unusually sweet, flowed less vigorously on a good sap morning than most trees, and continued flowing after the other trees had ceased during a warm spell. I suspect that here the protoplasm

was simply less responsive and less sensitive, less influenced by the rise in temperature, and much slower to recover after stimulation. In this way probably much of the observed individuality existing between different maple trees may be accounted for.

The quantity of sugar in the sap of any tree would be no indication of the difference in permeability, that is of pressure. This sugar content depends upon the total quantity of starch stored in the pith rays and the rapidity of conversion as well as on the permeability. The relatively greater quantity in the sap of the outer wood over that from the inner layers, on the other hand, would probably be proportional to the amount of pressure and flow.

The flow is not always as great as the pressure would lead one to expect. This may be because in these cases the available supply of water in the wood is less than usual.

Since each annual cylinder of wood with its system of vessels is in the form of a cone each extending higher on the tree than the preceding, water would probably tend to pass from the shorter layers to the higher ones, thus helping to raise the water in the tree. Water for the inner layers would probably be drawn primarily from the soil. Pressure in the twigs and branches is usually much less than in the lower trunk. This may be for three reasons, *viz.*,— because the temperature would equalize so quickly, because the radial chains of pith-ray cells would be shorter than in the trunk, or because of a less unequal permeability in the cells of the twigs. When a small branch or twig is cut off, sap flows from both surfaces but under no great pressure. I believe that the main portion of the flow in severed branches is due to the compressed air caused by the forcing up of sap into this part of the branch from the wood below.

Sugar probably passes from the wood fibers from the longitudinal faces if unequal temperature affects them in a similar manner, and owing to the narrow diameter of the fibers the flow thus caused would probably return again to the other side of the fibers without causing much, if any, pressure.

An objection to this theory which quickly comes to one's mind is the following. Why should the excreted sap pass through the pits into the next cell rather than around back between the plasma

membrane and the cell wall to the other end of the cell, thus producing a flow back through the cell without evident pressure? This seems impossible to answer at the present state of our knowledge, but it must be remembered that all theories of pressure produced by unequal permeability must meet this same objection. I believe, however, that a more critical study of the cell will eventually settle this point.

Regarding the water in the inner and outer layers, the Vermont *Bulletin* gives determinations up to a depth of 15 cm. only, and these are the only ones available. It was found on December 13th that the water content of the outer wood was considerably greater than the inner (37.5% and 24%). From that time until March 11th the percent in the outer layers decreased to 33.4% while that of the inner wood increased to 39.1%, thus giving a greater percentage for the inner layers. From then until April 28th there was an increase in both layers, but principally in the inner. At about this time the buds began to open and the water content of both fell abruptly. Along toward the first of June the content of the outer layers again became greater than the inner for a few weeks. These results seemed at first to present an objection to the present theory in that one would expect a greater water content in the outer layers into which the water would be forced from the deeper wood by the pumping action of the pith rays. After further thought, however, I am inclined to believe that the above readings are to be expected. The outer layers are subjected alternately to much greater pressures and suctions, while farther within the fluctuations are moderate, with predominating suction. It is reasonable to suppose that such violent fluctuations would gradually cause the accumulation of gas in these outer layers, and especially since these are near the exterior.

Why this particular temperature of from 1° to 3° C. should be so efficient in causing abrupt stimulation rather than any other is also an unsolved question. It must be noted, however, that several other phenomena seem to be connected more or less definitely with the same temperature, namely the exudation of water from the surface of Spirogyra threads already mentioned, and the gradual death of Coleus and other tender plants when subjected to this temperature but not frozen. This being the

temperature at which pure water is at its greatest density suggests that a re-arrangement of molecules in the water might be the source of the stimulus. The objection to this is that only pure water has this point of maximum density while in solutions of but slight concentration the point rapidly approaches the freezing point, and soon these two are identical.

It must be borne in mind that the idea that pressure is due to unequal permeability as above outlined is theory, not demonstrated fact. Its usefulness should lie in directing future investigation.

Trees that Bleed Late in Spring

Trees of this second group show quite a different behavior in regard to the environmental factors, especially temperature. In general the seasonal flow steadily increases from its inception until the maximum is reached and then as gradually declines. The composition of the sap of the different species differs according to the date of flow, and especially the time of beginning. There is little similarity in the composition of the sap in the different species. That of birch contains a large percent (6 %) of sugar, but this is glucose, not cane sugar, while that of the grape is almost pure water and contains no sugar. If trees of this class are cut down, the stump surface will continue to bleed, in the birch and grape very freely, while the cut surface of the trunk will soon become dry.

According to Clark, the black birch begins to bleed about April 1, attains its maximum the last of April, and stops about the middle of May. The wild grape commences about May 1st, arrives at its maximum of flow and pressure about May 30th, and ceases early in June. The pressure and flow in both of these plants fluctuates very little as compared with the maple, and depends very little on the temperature of the air. Great changes in temperature affect the pressure slightly, but only after several hours. Nearly the whole fluctuation consists in a regular diurnal periodicity greatest at night and less in the morning. In this group of trees the phenomenon is without doubt one of root pressure, and the fluctuations are characteristic root pressure fluctuations.

According to Clark, holes bored at different heights in a birch tree showed that the column of sap was supported almost entirely by the pressure from the root at the base.

The difference between the bleeding phenomena of the group of trees which bleed in late spring, and then mainly from the root, and the trees of the maple type is, after all, perhaps mainly one of degree only. Although in early spring there is no bleeding from the root but rather suction in the maple, later in April when the leaves are about to appear, root activity is evident here also, though always moderate. Eliminating the peculiar earlier stem pressure the condition in the maple would be normal for the other group. In the case of young maple saplings the root activity begins considerably earlier than in large trees, probably due to the shallower root system. This also happens in the roots of young birch saplings. In the case of these young maple saplings I am inclined to believe that the flow was perhaps entirely due to root pressure.

On the other hand, the conversion of starch in the trunk and branch cells of the birch tree may take place at a later date than in the maple and without the accompanying spasmodic changes in the permeability of the membranes. Conversion seems to commence in the root in this case and progress upward, but this point has not been definitely proven. It seems more natural to expect the starch of the trunk in these trees as well as in the maple to be converted before that in the roots owing to the retarding effect of the slowly warming soil. Whether the trunk tissues of birch take part in producing pressure late in the season has not been carefully investigated. From the experiments of Clark it seems rather doubtful. As we have already learned, pressure is not a necessary accompaniment of the escape of sugar from living cells into the vessels.

If we accept the cell-activity theory for the sap flow in the maple as the most probable, then it seems likely that the difference between the trunk cells of birch and the other trees of this group and those of the maple lies in the inability of the temperature or any other stimulus to cause unequal permeability of the proper nature (*i. e.*, with the proper mechanism) to cause pressure. Therefore the only pressure evident in the birch is the so called root pressure.

Owing to the difference in structure between roots and stems the exact mechanism having to do with the root exudation phenomena in all these trees is a different problem, and not to be discussed here.

Molisch [1] has recently come to the conclusion that many cases of bleeding in trees through tap-holes or other wounds are local, and exist only after the incision is made. The wound here acts as a stimulus starting repair phenomena, with increased turgidity of the neighboring cells. He is inclined to believe, however, that the spring flows in maple, birch, and grape are general phenomena and of another category. To me it also seems that the conditions outlined at the beginning of this paper rather preclude the consideration of the maple phenomena as local. But I cannot see that the fact that they were local would in any way preclude the action of the pith rays as here outlined.

Summary

1. The source of pressure for the bleeding of trees in spring seems to be localized in different portions of the plant in different species.

2. Trees may be roughly classified into two groups in this regard: (*a*) those in which the source is mainly in the trunk and branches. These, as for example the maple, bleed early in the season. (*b*) Those in which the source is in the root only. These bleed later in the spring, as for example the birch and grape.

3. Only the problem of the cause of pressure in the maple is considered in this paper.

4. There seems to be an undoubted relation between the occurrence of pressure in the maple and the fluctuations in temperature.

5. In connection with no other fluctuating factor of the environment can such relation be shown.

6. Pressure exists only when the temperature is rising. When it falls or remains constant, suction occurs.

[1] Molisch, H. "Ueber localen Blutungsdruck und seine Ursachen." *Bot. Zeit.*, vol. 60, p. 45, 1902.

7. Except when the temperature is rising past the vicinity of 0° C. the pressure is very moderate or slight. In the latter case, however, it may rise to the height of from 6 to 9 kg. per sq. in. in less than one and one half hours. Pressure then begins to fall whether or not the temperature still continues to rise.

8. The flow is in a general way coincident with, and proportional to, the pressure.

9. Expansion of gas in the wood can by no means account for the amount of pressure exhibited by the maple; and such expansion is likewise probably incapable of accounting for the total amount of flow.

10. Water expansion in the wood, while it can readily account for the pressure, if confined, is probably not so closely confined, and at any rate is incapable of accounting for the volume of flow.

11. The expansion of the wood can account for the pressure only when the sap is confined, and such complete confinement is highly improbable. It cannot account for the volume of flow.

12. No combination of these theories can produce a sufficient explanation of both pressure and flow.

13. Freezing is not capable of accounting for the phenomenon.

14. The only theory so far advanced that can account for all the observed phenomena is the living-cell theory. This seems in most respects satisfactory.

15. Living cells could produce pressure by contraction only when the outlet of the cell is unconnected with the chamber immediately around the contracting membrane. The structure of the cell renders this improbable, and besides, the delicacy of the protoplasmic membrane precludes the formation of such high pressures by this means.

16. Osmotic phenomena seem the only resource. Only by flow through the cell from one reservoir to another, due to the unequal osmotic permeability at the two ends, does it seem possible to obtain pressure by this method. Osmosis in this way seems sufficient to account for even more than 9 kg. pressure.

17. The pith-ray cells seem the only ones in the wood in position to fulfil the above requirements.

18. The most probable explanation at present is that the pith-ray cells, stimulated by the rising temperature, become unequally

permeable thus setting up a current and accompanying pressure from the pith toward the bark.

19. The maple type seems to differ from the birch type principally in the localization of the active cells mainly in the trunk, rather than in the root; and in the spasmodic action of these under certain stimulation.

20. It is quite possible that careful research will show no such irritability in the butternut and other trees of this group as is found in the maple.

NOTES AND LITERATURE

TEACHING

McMurry's Special Method in Elementary Science[1] is by far the most comprehensive treatment of the subject which has appeared in this country, and must prove extremely useful to the teacher in the public schools. The first half of the book treats of the aims and method of the teaching of elementary science,— the author at first makes a brave attempt to call it nature study, but throughout the greater part of the book calls it science,— the second half offers model lessons and a very full list of topics for a graded course of study.

Mr. McMurry insists that the topics shall come from the pupil's close environment,— Professor Hodge has already suggested that a louse on a pupil's head might be used for an instructive lesson on vermin,— and he has introduced as a new feature many topics dealing with the application of science to life. A study of the principles which govern the great inventions as well as our homely household appliances, can be made to appeal strongly to children. The author insists that a generation trained in the elementary problems of sanitation, physiology, and hygiene will not fall such an easy prey to the patent medicine frauds, and will back up boards of health in the fight for pure food and clean streets.

Professor Jackman some time ago outlined a course of nature study in which topics from every field of physics, chemistry, astronomy, meteorology, physiography, and biology were coördinated. Mr. McMurry extends the field still further, so that the variety of subjects to be handled would, we should think, appal any but the most unusually well trained teacher. It is a pity that the importance of the right method does not stand out more clearly. Many teachers will continue to convey information in many fields instead of training powers of reasoning in one. Mr. McMurry of course insists on the well known truths which should govern methods in science teaching, and often expresses his truths forcibly, but this book like all his

[1] McMurry, Charles A. *Special Method in Elementary Science for the Common School.* New York, The Macmillan Co., 1905. 12 mo, ix + 275 pp.

others suffers from an astonishing obscurity of style and unskilful presentation. The trail of the German "Pedagogik" is over it all.

In the chapter on method the place of imagination in science teaching is discussed; "children, primary teachers and poets" are encouraged to use a certain amount of license. It is amusing in view of recent controversies to see Mr. Burroughs figure as an example of the imaginative school of nature students.

There is a very full list of books which serve as an aid in science teaching.

R. H.

EVOLUTION

Lotsy's Theories of Descent.[1]— This book is a series of twenty-one lectures delivered to students at the University of Leyden and designed "to awaken a desire for the investigation of questions relating to theories of descent." This aim it is well adapted to fulfil. The scope of the book is wide, and the discussions, while necessarily not exhaustive, never fail to be stimulating and to give the reader a view in perspective of a large part of the field of evolutionary thought and investigation. This is true in particular of the newer aspects of evolution, concerning which most of all a book of this sort was needed.

Lectures 1 and 2 are introductory in character. In them are discussed the limitations of evolution, the fact that it cannot explain everything, the beginning of the universe being quite beyond its sphere. The relation of science to religion is discussed and the absence of any real conflict between the two is shown; the ultimate questions of being and of consciousness are found to be beyond solution either by science or by religion. Lecture 3 deals with the origin of the earth, the newly discovered transmutation of one element into another, the origin of life and the fact that among organisms as among the elements one form may give rise to another. The dependence of organic form upon two sets of factors is noted, one set internal, the other external. Lecture 4 is devoted to the external factors or "morphogenic stimuli," such as light, heat, pressure, chemical composition

[1] Lotsy, J. P. *Vorlesungen über Deszendenztheorien mit besonderer Berücksichtigung der botanischen Seite der Frage. Teil I.* Jena, Gustav Fischer, 1906. 8vo, xii+384 pp., 2 pls., 124 text-figs.

of surrounding media, etc. Lecture 5 deals with adaptations and theories as to their origin, whether internal or external. Lectures 6 to 11 are on heredity. Spencer's comparison of heredity to regeneration of a broken crystal is shown to be incorrect by the fact of heteromorphosis among organisms. Nägeli's idioplasm theory and Weismann's germ plasm theory are shown to have been important as forerunners of the still more important ideas of de Vries, though all of these were anticipated in part by the work of Gregor Mendel. One of the lectures on heredity is devoted wholly to an exposition of Mendel's law (of alternative inheritance); another to variation curves, particularly to Galton's pioneer work in this field; another to filial regression, under which head are discussed the divergent views of Galton and Johannsen on regression, and the part played by the ancestors in the laws of heredity of Galton and Mendel respectively. In the final lecture on heredity the nature of the gametes (sex-cells) is shown to be the crucial question with theories of heredity, since in the gametes are contained all the internal factors of form. The phenomena of atavism, reversion, and latent inheritance (cryptomery, Tschermak) here come up for consideration.

Lecture 12 deals with the vexed question of the inheritance of acquired characters, which the author answers with a qualified affirmative; Lecture 13, with discontinuous variation as illustrated in the varieties of canary-birds, pigeons, and poultry, and among plants by numerous cases taken mostly from the works of de Vries and Korshinsky. Then follow two lectures devoted to the mutants of de Vries. In the next six lectures is given a historical survey of theories of evolution up to the time of Darwin, with a brief account of Darwin's life. In a subsequent volume the author proposes to discuss the Darwinian theory and the post-Darwinian literature.

The volume already issued is a marvel of prompt publication admirably done. The preface is dated September 11, 1905, and the plates contain half-tone illustrations made from photographs taken in September, 1905. Three months later the finished work is delivered in America, yet no evidence of haste is seen in the execution of the work; it is up to the usual standard of Fischer's publications, which statement in itself is sufficient praise.

W. E. C.

EXPLORATION

Scott's Voyage of the 'Discovery'.[1]— At the beginning of the seventeenth century, knowledge of the Antarctic regions was so meager that Quiros, a Portuguese favored by Pope Clement VIII, obtained permission from Phillip III, the King of Spain, to "prosecute a voyage to annex the South Polar continent and to convert its inhabitants to the true faith." Quiros never reached the Antarctic Circle but since that time, the occasional visits of navigators have added slightly to our scanty knowledge of this distant part of the earth, although real scientific work did not begin until the middle of the eighteenth century, when, in 1773, James Cook, with two vessels especially fitted for exploration, first crossed the Antarctic Circle. About 1820, Bellingshausen discovered the first known land (Peter Island) within the Antarctic Circle, and later in the century other expeditions touched at various points of the Antarctic continent and brought back more or less fragmentary and imperfect accounts of that region.

The last decade has seen great activity and interest in the investigation of this area, so that in 1901 no less than three expeditions, working in coöperation, were sent out to undertake a more exact study of the Antarctic seas and lands. The German expedition was led by Drygalski, the Swedish was in charge of Dr. O. Nordenskjöld, while the third, under the auspices of the Royal Geographical Society of London was commanded by Captain Robert F. Scott, R. N. The two volumes here reviewed, present a straightforward narrative of the work of the English party as modestly told by Captain Scott himself.

The preliminary chapters deal briefly with the previous explorations, the circumstances leading up to the organization of the expedition, the construction of the *Discovery* especially built for hard work in the ice, the equipment of the vessel, and the personnel of her officers and crew.

Sailing from England in July, 1901, the *Discovery* reached New Zealand in due course and on December 24, following, steered south for Victoria Land, the portion of the Antarctic continent assigned to this expedition for exploration. The remainder of the short polar

[1] Scott, Robert F. *The Voyage of the 'Discovery.'* New York and London, Charles Scribner's Sons, 1905. 8vo, 2 vols., illus. $10.00.

summer was spent in a preliminary reconnaissance of the coastline and the final selection of a favorable wintering spot in McMurdo Sound to the southeast of the volcanoes Erebus and Terror. Much of the coast thus visited was practically unknown and new land was discovered to the west of the Great Ice Barrier and was named King Edward VII Land. It was also determined that the Ice Barrier at this point had receded since the time of Ross's visit in 1841–2, and that the volcanoes Erebus (active) and Terror are upon an island.

In February, 1902, the *Discovery* anchored in the spot selected for winter quarters. Huts were erected on shore for the magnetic instruments and the routine of general scientific work was at once inaugurated. By the last of March, 1902, the vessel was frozen solidly into the ice, and throughout the Antarctic winter the scientific work was continued without interruption. By the first of November following, with the return of the sun, Captain Scott, Dr. E. A. Wilson, and Shackleton started on an extended sledge journey to the south. This party, traversing the surface of the Great Ice Barrier, followed south along the range of mountains that evidently represents the rugged coastline at this point, and after untold hardships returned at the end of three months having reached latitude 82° 16′ 33″ S., the most southern point ever attained by human beings. At this turning place, a lofty mountain was seen to the southwest and named Mt. Markham (15,100 ft.) while other great ranges stretched away to the south-southeast.

A second winter was spent in McMurdo Sound as the ice did not release the *Discovery* from its winter quarters. The little company was in good condition for the second season and the arrival of the relief ship *Morning* made it possible to recruit certain stores for another summer's work. This consisted chiefly in an expedition to the west to explore the Ferrar Glacier and the great tableland beyond which was found to rise for some 9000 feet. Over this inhospitable area Captain Scott and two other picked men made a remarkable journey on foot, and found it a "vast plain.... the most desolate region in the world," barren, deserted, windswept, and piercingly cold. The glacier and the Great Ice Barrier appear to be parts of the slowly receding outskirts of a polar ice cap that formerly was far more extensive.

By February of the following year, the ice floe broke up and the *Discovery*, in company with two relief ships, was enabled to return to New Zealand and thence home to England.

In his closing chapters, Captain Scott makes a few general remarks

on the nature of the land masses, the ice, and the ocean currents of these seas, and the two appendices by Ferrar and Wilson respectively, give a brief account of the geology and of the larger vertebrates. The observations on the penguins are of particular interest. The breeding grounds of the Emperor Penguin were for the first time discovered and valuable observations on the breeding habits were made at Cape Crozier where a small rookery was found. With respect to the so called 'pouch' of this and the King Penguin in which the egg is said to be carried, Dr. Wilson writes: "We are agreed that the term 'pouch' which has been used in this connection, is one which not only does not describe the matter, but is anatomically wrong and misleading. The single egg, or the chick, sits resting on the *dorsum* of the foot, wedged in between the legs and the lower abdomen; and over it falls a fold of heavily feathered skin, which is very loose, and can completely cover up and hide the egg or chick from view." This appearance is excellently shown in an accompanying photograph.

Although the scientific results have not yet been fully published, it seems certain that they will be the most valuable hitherto obtained by any Antarctic expedition.

The two handsome volumes of this work are well printed and abundantly illustrated with remarkably clear photographs as well as by numerous colored plates from sketches by Dr. Wilson. Two folding charts show in detail the coast of Victoria Land, the new land features discovered, and the routes taken in exploration. As a convenient method of keeping the reader informed of the lapse of time during the course of the narrative, the month and year corresponding to the time of the incident related, are printed at the upper inside margin of each page. The narrative itself is of intense and absorbing interest to the naturalist and the general reader alike, and is recommended to any who may be skeptical of the value of polar exploration. For in the author's own words: "The voyage of the '*Discovery*' was not conducted in a spirit of pure adventure, but we strove to add, and succeeded in adding, something to the sum of human knowledge."

G. M. A.

BOTANY

Anther Dehiscence.[1]—A study was begun in 1901 in connection with an article on the pollination of Solanum and Cassia, published in the *Kansas University Science Bulletin*, and continued in 1903 in a thesis presented to the faculty of Washington University for the degree of doctor of philosophy. The author recognizes seven types of apically dehiscent anthers and designates them as araceous, gramineous, polygalaceous, ericaceous, dilleniaceous, Solanum-Cassia, and melastomataceous. First, these types are defined and the families and genera representative of each are indicated. Then there follows an account of the floral ecology of the forms, except of the first four types. Seven tables give the results of the arrangement of the data relating to the geographical distribution of the genera of the several types, and one shows the distribution of the flowering plants in general. Fourteen geographical regions are recognized, based on the floristic regions of Drude. The Tropical American Region shows a maximum of Phanerogamia, the Indian Region being second.

The dilleniaceous, Solanum-Cassia, and melastomataceous types have the corolla, or at least the limb, widely patent, and the anthers basifixed and usually linear.

In the dilleniaceous type the stamens are indefinite, the anthers usually elongate, the flowers usually actinomorphic and highly colored. To this type are assigned 16 genera belonging to 6 families: five genera of Dilleniaceæ, five of Elæocarpaceæ, three of Ochnaceæ, one each of Theaceæ, Bixaceæ, and Flacourtiaceæ. An Indian maximum is indicated for this type, the Tropical American and Australian Regions being next with the same number of genera; the Tropical American Region, however, shows more species than the Australian. As visitors there have been observed: bees — Xylocopa, Euglossa, Bombus, Apis, Melipona, Halictus, Centris, Podalirius; birds — a brush-tongued paroquet, Charmosyna, a honey-sucker, Myzomela; flies — Muscidæ.

The Solanum-Cassia type differs from the dilleniaceous in the stamens being fewer and the filaments short. In this category fall

[1]Harris, J. Arthur. "The Dehiscence of Anthers by Apical Pores." From the *Sixteenth Annual Report of the Missouri Botanical Garden*, pp. 167–257, issued May 31, 1905.

59 genera belonging to 19 families, 6 of which are Monocotyledons. The Monocotyledons are: one genus of Mayacaceæ, six of Rapateaceæ, two of Commelinaceæ, one of Pontederiaceæ, five of Liliaceæ, four of Amaryllidaceæ. The Dicotyledons are: one genus of Pittosporaceæ, nine of Leguminosæ, three of Tremandraceæ, four of Sterculiaceæ, eleven of Ochnaceæ, two of Dipterocarpaceæ, one of Flacourtiaceæ, sections of Begonia in Begoniaceæ, sections of Ardisia in Myrsinaceæ, one of Loganiaceæ, two each of Gentianaceæ Solanaceæ, and Rubiaceæ. The table for the Solanum-Cassia type shows a maximum for the Tropical American Region, with the Australian Region second. Genera of visitors observed on flowers of this type are: bees — Osmia, Megachile, Ceratina, Xylocopa, Euglossa, Bombus, Apis, Trigona, Melipona, Halictus, Augochlora, Megacilissa, Melissodes, Podalirius, Centris, Oxæa; flies — Rhingia, Volucella; butterflies — Argynnis; birds — Mimus, Nectarinia, Chlorostilbon.

The melastomataceous type differs from the preceding mainly in the long filaments and in both locules of the anther usually opening through a single pore. Of the 161 genera of Melastomataceæ it includes all except 12, besides one genus of Leguminosæ and two of Bixaceæ. The Tropical American Region contains about 63 % of plants of the melastomataceous type, the Indian Region showing about 20 %. The observed visitors are: bees — Xylocopa, Bombus, Trigona, Halictus, Centris; flies — Syrphidæ; beetles — Cetonia, Buprestis; birds — Trochilidæ.

The table of genera of the three types shows a Tropical American maximum of about 57 %, and an Indian elevation of about 21 %. In Apidæ the Tropical American Region is first, with 64 genera of bees, the Mediterranean-Oriental Region second, with 51, the Northern Region third, with 50. Table J shows the distribution of Hymenoptera of all genera. K shows the relative abundance of genera of Apidæ. Diagram L gives curves for the distribution of endemic genera of the apically dehiscent types, of the Phanerogamia, of the Apidæ, and of all Hymenoptera. Diagram M shows the relative distribution of all genera of the same groups.

These curves indicate a direct relationship between the geographical distribution of the Apidæ and of the dilleniaceous, Solanum-Cassia, and melastomataceous floral types.

C. Robertson

Freeman's Minnesota Plant Diseases.[1] — Simplicity, attractiveness, and full illustration are among the qualities of an ideal publication on agricultural science if it is to reach the people without the intervention of a middle-man. These qualities are possessed by a recent book on the diseases of plants prepared by Professor Freeman under the direction of the Geological and Natural History Survey of Minnesota,— a State which spends large sums annually on the study of its native resources and limitations, but the Agricultural Experiment Station of which is said never to have employed a special plant pathologist. The treatment falls under three general heads: fungi and their life history; economic applications; and diseases of plants. The book is likely to realize its author's hope of making the intelligent farmer who may read it an intelligent observer and assistant to the expert investigator.

W. T.

Ward's Flowers of English Trees and Shrubs.[2]— This volume, the third in the author's work on trees, is devoted to a study of the flowers and inflorescences of the woody plants of England. It is essentially a book for the layman. It is to be recommended for its freedom from those grievous errors which so often characterize the "popular" books of a certain class of literary aspirants in this country. The amateur student will receive all the aid and instruction he needs, while the technical student will find a large amount of valuable material presented in a lucid and concise form.

The first part of the book is general and is devoted to a study of the more common types of flowers and inflorescences. The reader is first introduced, by means of a few well chosen examples, to the typical inflorescences and then to their variations. There next follows a treatment of the flower, its different parts, their nature and development. The general part of the book concludes with two chapters on the ecology of the flower. Naturally, these chapters concern themselves with the process of pollination and the characters of the flower which are correlated therewith. The entire material of Part I is admirably selected and lucidly set forth.

The second part of the book is special and takes the form of a man-

[1] Freeman, E. M. *Minnesota Plant Diseases.— Report of the Survey, Botanical Series*, v. St. Paul, published by the Regents of the University, July 31, 1905. 8vo, xviii + 432 pp., 211 figs.

[2] Ward, H. Marshall. *Trees, Vol. III. Flowers and Inflorescences.* Cambridge, University Press, 1905. 12mo., 402 pp., 142 figs.

ual for the classification of the common English trees, based upon their flowers and inflorescences. The willows are treated separately in an appendix. Tables are there given for the classification of willows when pistillate or staminate catkins are alone available.

The book is concluded with a copious glossary which defines the technical terms necessarily used in a book of this sort.

H. S. R.

Notes.— Dr. Scott's Wilde lecture on the "Early History of Seed-bearing Plants as Recorded in the Carboniferous Flora" is published, with illustrations, in vol. 49, part 3, of the *Memoirs and Proceedings of the Manchester Literary and Philosophical Society.*

The classification of Monocotyledons is further discussed by Delpino in series 5, vol. 10, of the *Memorie della R. Accademia delle Scienze* of Bologna.

A short illustrated note on the bark characters of trees, by Peet, is contained in *The Country Calendar* for November, 1905.

An address on plant morphology and taxonomy, by Kraemer, is published in the *American Journal of Pharmacy* for September, 1905.

A paper on contractile vacuoles and the frothy structure of protoplasm, by Degen, forms Heft 9–11, Abteilung 1, of the *Botanische Zeitung* for 1905.

Lindemuth (*Die Gartenwelt*, Oct. 28, 1905) has propagated Rex begonias from the leaves with long petioles. The petiole strikes root from the base and produces a crown of leaves at the tip. The petiole undergoes no great modification in form or structure except to increase somewhat in size but it may function as the stem of the plant for a long period of time.

The influence of color in floral ecology is analyzed in a paper by Delpino forming part of series 6, vol. 1, of the *Memoire della R. Accademia delle Scienze* of Bologna.

Studies on the composition and metabolism of apples, by Bigelow, Gore, and Howard, form *Bulletin 94* of the Bureau of Chemistry, U. S. Department of Agriculture.

The influence of environment upon the composition of the sugar beet is discussed by Wiley in *Bulletin 95* of the Bureau of Chemistry, U. S. Department of Agriculture.

The variability of wheat varieties in resistance to toxic salts is the subject of *Bulletin 79* of the Bureau of Plant Industry, U. S. Department of Agriculture.

A paper on the vitality of buried seeds, by Duvel, forms *Bulletin 83* of the Bureau of Plant Industry, U. S. Department of Agriculture.

A mechanical study of thistle-down as a parachute is published by Dandeno in *Science* of November 3, 1905.

Figures of some natural tree grafts are published by M. P. Wheeler in *The American Inventor* for November.

An analysis of the plant geography of Canada, by Drummond, appears in vol. 8, part 1, of the *Transactions of the Canadian Institute.*

Plants characterizing the life zones of Texas are listed by Bailey in *North American Fauna,* no. 25.

The forest conditions of the Gila River Forest Reserve, N. M., are discussed by Rixon in *Professional Paper 39* of the U. S. Geological Survey.

A note on G. J. Graham and his Mexican collections of 1827–9 is published by Britten in *The Journal of Botany* for November.

A popular account of Mexican vegetation, with instructive habit photograms, is published by Purpus in *Möller's Deutsche Gärtner-Zeitung* of October 7.

Five new Mexican flowering plants are described by Rose in no. 1427 of the *Proceedings of the U. S. National Museum ;* a new monotypic genus (Harperia) of Umbelliferæ and a new Zizia, from Georgia, are described by the same author in no. 1428 of the same publication, and Rose and House describe three Mexican violets (one new) in the succeeding no. 1429.

Part 7 of Captain J. Donnell Smith's *Enumeratio Plantarum Guatemalensium* has recently been distributed by the author.

The grasslands of the South Alaska coast are discussed by Piper in *Bulletin 82* of the Bureau of Plant Industry, U. S. Department of Agriculture.

The relations of the floras of the Northern Atlantic, the Polar Sea, and the Northern Pacific are considered by Simmons in Bd. 19, Heft 1, of the second Abteilung of *Beihefte zum botanischen Centralblatt.*

De Wildeman has begun the publication, through the Government of the État Indépendant du Congo, of an illustrated enumeration of the plants collected by Laurent during his Congo mission of 1903–04.

Important papers on Australasian botany are contained in current issues of *Proceedings of the Linnean Society of New South Wales* and the biological section of the *Reports of the Australasian Association for the Advancement of Science.*

Ridley has papers on Gesneraceæ of the Malay Peninsula, Aroids of Borneo, and New and Little-known Malayan Plants — II, in no. 44 of the *Journal of the Straits Branch of the Royal Asiatic Society,* issued in July last.

Cooke's *Flora of the Presidency of Bombay,* in vol. 2, part 2, issued in July last, reaches into the Verbenaceæ.

Schlotterbeck and Blome contribute a paper on the chemistry of *Bocconia cordata* to the *Pharmaceutical Review* for October, 1905.

A morphological and anatomical study of Claytonia, by Holm, forms vol. 10, no. 2, of the *Memoirs of the National Academy of Sciences.*

Britten publishes a note on Cliftonia in *The Journal of Botany* for October, 1905.

Interesting statistics of the cotton production and valuation of the world are furnished by Watkins in *Bulletin 34* of the Bureau of Statistics, U. S. Department of Agriculture.

An account of "Cratægus in Eastern Pennsylvania," distributed by Sargent on September 22 from the *Proceedings of the Academy of Natural Sciences of Philadelphia* for 1905, gives keys to the groups and species represented, of which latter 82, with 3 distinct varieties, are included,— 46 of the species being described as new.

A paper on Opuntia, by Berger, is contained in Engler's *Botanische Jahrbücher* of November 10, 1905.

Townsendia wilcoxiana is figured in vol. 5, fascicle 3, of *Icones Selectæ Horti Thenensis.*

Antennaria neodioica gaspensis is a new form from eastern Quebec, described by Fernald in *The Ottawa Naturalist* for November.

Power and Barrowcliff discuss the seed constituents of Hydnocarpus and Gynocardia in nos. 54 and 55, respectively, of the publications of the Wellcome Chemical Research Laboratories, of London.

An illustrated account of *Solanum commersonii* is contained in *Gartenflora* of September 1, 1905.

A chemical analysis of *Tecoma mollis*, by Kebler and Seidell, forms *Circular 24* of the Bureau of Chemistry, U. S. Department of Agriculture.

Illustrated articles on mangroves are contributed by J. A. Dimock and A. W. Dimock to *Country Life in America* for November, 1905.

Warburg gives an account of Phthirusa and Strutanthus — the mistletoes of rubber — in *Der Tropenpflanzer* for November, 1905.

Five additional species, and two varieties, are added to the hitherto monotypic genus Osmaronia by Greene in the concluding signature of *Pittonia*, vol. 5.

Habit figures of *Grammatophyllum speciosum*, a giant orchid, are given by Ridley in the May number of the *Agricultural Bulletin of the Straits and Federated Malay States*.

The somewhat aberrant nomenclature needs of orchid hybrids are discussed by Bohlmann in *Die Gartenwelt* of November 11, 1905.

The Xanthosomas cultivated under the name Yautia form the subject of *Bulletin 6* of the Porto Rico Agricultural Experiment Station, issued in English and Spanish.

No. 24 of Holm's "Studies in the Cyperaceæ," published in *The American Journal of Science* for September, 1905, deals with new or little known Carices from northwest America.

A well illustrated monograph of the wild and cultivated grasses of Iowa, by Pammel, Ball, and Lamson-Scribner, forming part 2 of "The Grasses of Iowa," has been issued as a *Supplementary Report of the Iowa Geological Survey*.

"Poa and its Commercial Fruit Characters" is the subject of *Bulletin 84* of the Bureau of Plant Industry, U. S. Department of Agriculture by Brown and Hillman.

Cavendish reports, in *The Indian Forester* for August, that after an interval of some 30 years *Dendrocalamus hamiltonii* has flowered throughout the Assam district in the wholesale fashion characteristic of the bamboos.

The storage and germination of Zizania seed is the subject of *Bulletin 90, part 1*, of the Bureau of Plant Industry, U. S. Department of Agriculture.

A Spanish hybrid of *Juniperus phœnicea* and *J. communis* is described by Cadeval y Diars in vol. 5, no. 12, of the current series of *Memorias de la Real Academia de Ciencias y Artes de Barcelona.*

The third and concluding volume of Braithwaite's *British Moss Flora* has recently appeared from Reeve's of London.

A new *Index Filicum*, by Christensen, is being issued in fascicles from the Hagerup press of Copenhagen. All of the pteridophyte names published from 1753 to 1905 are included, the treatment being much as in the *Index Kewensis* devoted to spermatophytes.

An extensive paper on the anatomy of *Acrostichum aureum* is published by Ethel A. Thomas in *The New Phytologist* of October 25, 1905.

A new fern (*Polystichum krugii*) from Porto Rico is described by Maxon in the *Proceedings of the Biological Society of Washington* for October 17, 1905.

Laing contributes a revised list of New Zealand seaweeds, and the first part of an account of the Ceramiaceæ of the island, to vol. 37 of the *Transactions and Proceedings of the New Zealand Institute,*— which contains numerous other botanical papers of interest.

A series of 64 unusually good three-color plates illustrates Dumée's *Nouvel Atlas de Poche des Champignons Comestibles et Vénéneux,* recently published by Klincksieck of Paris.

Publication no. 28 of the Bureau of Government Laboratories, Manila, consists of papers by Copeland on "The Polypodiaceæ of the Philippine Islands" and "New Species of Edible Philippine Fungi."

Under the title *Die Pilze von Tirol, Vorarlberg, und Lichtenstein,* Magnus has published, through the Wagner press of Innsbruck, a volume of 716 pages containing an account of over 3500 species, with bibliography, notes on synonymy, habitat, etc. The very full indexes alone occupy over 100 pages.

A voluminous catalogue of the fungi of the Low Countries, by the venerable Oudemans, constitutes vol. 12 of the second section of *Verhandelingen der Koninklijke Akademie van Wetenschappen* of Amsterdam.

An account of Norwegian Hymenomycetes, begun by Blytt and finished by Rostrup, has been separately issued from the *Videnskabs-Selskabets Skrifter* of Christiania, for 1904.

Guzmán enumerates 40 Salvadorean oil plants, cultivated or wild, in vol. 2, no. 14, of the *Anales del Museo Nacional* of El Salvador.

The destructive occurrence of *Trametes pini* in India is noted by Mayes in *The Indian Forester* for July, 1905.

Mushroom-growing and tissue-culture spawn production are described by Duggar in *Bulletin 85* of the Bureau of Plant Industry, U. S. Department of Agriculture.

A twin specimen of *Geaster fornicatus* is figured in the *Gardeners' Chronicle* of November 4, 1905.

The nuclear and sexual phenomena of Phyllactinia and other mildews are described by Harper in the recently issued *Publication no. 37 of the Carnegie Institution of Washington.*

A paper on the Monoblepharideæ, by Woronin, forms vol. 16, no. 4, of the *Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg.*

A note on the Tuberaceæ of Portugal is published by Mattirolo in the *Atti della R. Accademia dei Lincei, Roma,* of October 15, 1905.

Uncinula conidiigena is the name of a new parasite of *Populus termula*, described and figured by Cocconi in series 5, vol. 10, of the *Memorie della R. Accademia delle Scienze* of Bologna.

Uromycladium is the name proposed by McAlpine for a genus of South Pacific leguminous rusts, related to Uromyces and Ravenelia, in *Annales Mycologici* for August, 1905.

The Japanese species of Uromyces on Sophora and Cladrastis are analyzed by Kusano in the (Tokyo) *Botanical Magazine* of August 20, 1905.

An account of endophytic adaptation shown by *Erysiphe graminis* under cultural conditions, is given by Salmon in vol. 198, series B, of the *Philosophical Transactions of the Royal Society of London.*

Diachæa cylindrica, a new Pennsylvanian species, is described by Bilgram in the current volume of *Proceedings of the Academy of Natural Sciences of Philadelphia.*

In a brochure recently issued from the Engelmann press of Leipzig, von Guttenberg considers the physiological anatomy of the galls produced by fungi.

Wheat improvement is considered by Lyon, in *Bulletin 78* of the Bureau of Plant Industry, U. S. Department of Agriculture.

The well known odor of moldy straw and hay is ascribed to a Streptothrix by Brocq-Rousseu in the *Revue Générale de Botanique* for October 15, 1905.

Hedgcock, in *Bulletin 90, part 2,* of the Bureau of Plant Industry, U. S. Department of Agriculture, differentiates the prevalent "crown gall" of apple trees into crown gall proper, and "hairy-root." The second is found not to be contagious, and the contagiousness of the first is not demonstrated.

A paper on the indigenous calabashes of Mexico, the Ayotli of Hernandez, is published in vol. 1, no. 2, of the *Anales de la Academia Mexicana.*

An illustrated article on Burbank and his work, by Honoria Tuomey, is contained in *Out West* for September, 1905.

Britten and Woodward have published some interesting correspondence concerning L'Heritier in recent numbers of *The Journal of Botany.*

Another of Fraser's Catalogues — this for 1796 — is reprinted in *The Journal of Botany* for November, 1905.

The recently issued 1904–05 *Report of the Government Botanist* for the Cape of Good Hope shows that the Cape herbarium now contains 44,189 sheets of specimens, of which 25,400 represent the Cape flora,— some 3000 of these being type sheets left by Harvey.

A new publication of the Tiflis Botanical Garden has been begun, under the title *Moniteur du Jardin Botanique de Tiflis.*

A series of illustrated articles on the London botanical gardens is being published by Perrédès in current numbers of the *American Journal of Pharmacy.*

A well illustrated account of the botanical garden at Buitenzorg is contributed by Ramaley to *The Popular Science Monthly* of November.

The Carnegie Laboratory at Tucson is described by Wittmack in *Gartenflora* of October 15, 1905.

An account of Dr. Kunze and his cactus collection, by Willey, is contained in *The American Inventor* for October, 1905.

Karasek gives an illustrated account of vegetation in the gardens of German Africa, in the *Wiener illustrierte Gartenzeitung* for November, 1905.

The Journals.— *The Botanical Gazette,* September: — Blakeslee, "Two Conidia-bearing Fungi"; Mottier, "The Development of the Heterotypic Chromosomes in Pollen Mother Cells"; Livingston, "Relation of Transpiration to Growth in Wheat"; Arthur, "Rusts on Compositæ from Mexico"; Shattuck, "A Morphological Study of *Ulmus americana*"; Billings, "Precursory Leaf-serrations of Ulmus"; Sheldon, "The Effect of Different Soils on the Development of the Carnation Rust."

The Botanical Gazette, October: — McCallum, "Regeneration in Plants — II"; Brown, "A Botanical Survey of the Huron River Valley — III"; Lyon, "The Spore Coats of Selaginella"; Schneider, "Contributions to the Biology of Rhizobia — V"; Eckerson, "The Physiological Constants of Plants Commonly used in American Botanical Laboratories — I"; Kraemer, "Further Observations on the Structure of the Starch Grain."

The Botanical Gazette, November: — Peirce and Randolph, "Studies of Irritability in Algæ"; Transeau, "The Bogs and Bog Flora of the Huron River Valley"; Ball, "Notes on North American Willows — I."

The Bryologist, November: — Haynes, "*Telaranea nematodes longifolia*"; Sargent, "Lichenology for Beginners — IV"; Chamberlain, "Some Common Errors"; Hill, "*Encalypta procera*"; Merrill, "Lichen Notes — I"; Holzinger, "A Note on Local Moss Distribution."

Bulletin of the Torrey Botanical Club, September: — Harper, "Phytogeographical Explorations in the Coastal Plain of Georgia in 1904"; Murrill, "The Polyporaceæ of North America — XII, A Synopsis of the White and Bright Colored Pileate Species"; Mackenzie, "Onosmodium."

Bulletin of the Torrey Botanical Club, October: — Cannon, "A New Method of Measuring the Transpiration of Plants in Place"; Harris, "The Fruit of Opuntia"; Abrams, "Studies on the Flora of Southern California"; Piper, "*Agropyron tenerum* and its Allies"; Cushman, "The Desmid Flora of Nantucket."

The Fern Bulletin, July: — Clute, "Species and Varieties among the Ferns"; Gilbert, "Observations on North American Pterido-

phytes"; Clute, "A Walking Shield Fern"; Gilbert, "Some Mexican Fernworts"; Terry, "More about the Ferns of Dorset"; Klugh, "*Nephrodium Boottii* or *N. spinulosum* × *cristatum*"; Eaton, "*Botrychium biternatum*."

The Journal of Mycology, July: — Morgan, "A New Species of Kalmusia"; Morgan, "*Peziza pubida*"; Davis, "A New Species of Synchytrium"; Holway, "North American Salvia-Rusts"; Clevenger, "Notes on some North American Phyllachoras"; Lawrence, "Blackspot Canker and Blackspot Apple Rot"; Sumstine, "*Gomphidius rhodoxanthus* once more"; Sherman, "The Host Plants of *Panæolus epimyces*"; Kellerman, "Notes from Mycological Literature — XVI," and "Index to North American Mycology."

Journal of the New York Botanical Garden, September: — Britton, "A Lost Species of Begonia [*B. rotundifolia*] apparently Rediscovered"; Hollick, "Palæobotanical Notes"; MacDougal, "Suwarro or Saguaro."

Mühlenbergia, vol. 1, no. 7: — Heller, "The Western Veratrums," and "A New Linanthus."

Mühlenbergia, vol. 2, no. 1, is occupied by an account of botanical exploration in California during 1905, by the editor, Mr. Heller.

The Ohio Naturalist, November: — Surface, "Contribution to the Life History of *Sanguinaria canadensis*"; Schaffner, "The Classification of Plants — II"; Fischer, "An Abnormal Cone of *Pinus laricio*"; Gleason, "Notes from the Ohio State Herbarium — IV."

Appropriate space is devoted to botany in the *Ontario Natural Science Bulletin*, — the newly launched journal of the Wellington Field Naturalists' Club, of Guelph, Ontario.

The Plant World, August: — Bessey, "How much Plant Pathology ought a Teacher of Botany to know?"; Reed, "A Brief History of Ecological Work in Botany (Conclusion)"; Nehrling, "An Indian Magnolia [*Talauma hodgsoni*] in America."

The Plant World, September: — Atkinson, "Outlines for the Observation of some of the more Common Fungi"; Lloyd, "The Barley Cone — I. Some Points of Structure"; Kinney, "Outline of a Course in Plant Culture."

Rhodora, September: — Pease, "Notes on the Accentuation of Certain Generic Names"; Sargent, "Recently Recognized Species

of Cratægus in Eastern Canada and New England — VI"; Fernald, "*Symphoricarpos racemosus* and its Varieties in Eastern America"; Howe, "*Lotus tenuis* as a Waif in Rhode Island"; Collins, "Phycological Notes of the late Isaac Holden — I."

Rhodora, October: — Sanford, "*Eclipta alba* in Mass."; Sargent, "Recently Recognized Species of Cratægus in Eastern Canada and New England — VI (continued)"; Fernald, "An Anomalous Alpine Willow"; Lewis, "Sclerolepis in N. H."

The first volume of the *Proceedings of the American Breeders' Association*, containing an account of the St. Louis meeting of 1903 and the Champaign meeting of 1905, has recently been issued, and contains a large number of unusually practical and some theoretical articles on both animal and plant breeding.

Torreya, September: — Greene, "Origin of *Rhus bipinnata*"; Harris, "New Fasciations"; Tidestrom, "Note on *Botrychium virginianum*"; Harper, "Some Large Specimens of Small Trees in Ga."; Clark, "Cotyledon- and Leaf-structure in Certain Ranunculaceæ"; House, "*Lespedeza velutina* Bicknell a Homonym."

Torreya, October: — Tidestrom, "Notes on the Gray Polypody"; Lloyd, "The Artificial Induction of Leaf Formation in the Ocotillo"; Berry, "An Old Swamp-Bottom"; Harper, "*Mesadenia lanceolata* and its Allies."

Zoe, August: — T. S. Brandegee, "A Collection of Mexican Plants"; "Palms of Baja California"; "A New Calamintha"; "Plants from Sinaloa, Mexico"; Greenman, "New Species of Mexican Plants"; Katharine Brandegee, "Notes on Cacteæ."

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THE AMERICAN NATURALIST

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CONTENTS

		Page
I.	**Adaptive Modifications of Occipital Condyles in Mammalia** . . C. S. MEAD	475
II.	**Living and Fossil Species of Comptonia** . . . . . E. W. BERRY	485
III.	**Notes and Literature**: *Paleontology*, Jordan's Guide to the Study of Fishes, Lankester's Extinct Animals, Notes; *Geology*, Ries's Economic Geology of the United States, Notes	525
IV.	**Correspondence**: The Danish Arctic Station	535

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AMERICAN NATURALIST

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ADAPTIVE MODIFICATIONS OF OCCIPITAL CONDYLES IN MAMMALIA

CHARLES S. MEAD

HISTORICAL

A NUMBER of papers have been written on the occipital condyles but they deal with them from either an ontogenetic or a phylogenetic standpoint. Osborn (:00) has shown that certain of the mammals, such as Tachyglossus (Echidna) and Cercoleptes, possess but a single tripartite condyle continuous across the median plane by a narrow bridge; that others, such as Lutra, have the condyles widely separated and that between these two extremes there are intermediate stages, showing thus that the "mammalian occipital condyles arose from a reptilian tripartite type by the reduction of the median basioccipital element and the expansion of the lateral exoccipital elements."

Gadow (:02), from a study of the anterior cervical vertebræ in the various vertebrates, comes to the conclusion that "the original craniocervical joint must have been a paired one, formed by the lateral occipitals with their more or less serially homologous parts, the neural arches of the first free vertebra. A single condyle could be formed only after the centrum of the first vertebra had been withdrawn as the odontoid process, so as to let the neural arches and the ventral unpaired piece of the atlas . . . . form a cup." Hence he reverses Osborn's order and looks upon the "monocondylar, essentially basioccipital knob, as the final outcome of evolution, independently arrived at by various groups of Sauropsida."

The origin of the condyles needs to be examined further from

this point of view, attention being paid especially to the "proatlas" which Broom (:03) has described in Gomphognathus and Trirachodon. It also occurs in the Rhynchocephalia and the Crocodilia, and Broom predicts that it will yet be found in most of the primitive reptilian types.

Fischer (:01) has shown that in the embryo of the European mole (*Talpa europæa*) the lateral condyles are confluent around the base of the foramen magnum, while in the adult they are separate. He apparently supports Osborn's position in the following sentence: "The most important thing to me is the fact that the configuration of the occipital joint in our mole occupies a sort of intermediate position between the mammals and the Sauropsida."

From a study of the chondrocranium of *Lacerta agilis*, Gaupp (:00) directly supports Osborn. He finds four craniovertebral connections: a dorso-median (the ligamentum apicis dentis), the two lateral corresponding with the lateral condyles of the mammals, and a ventro-median (the median basioccipital element of Osborn) which connects the two lateral parts in the Sauropsida, but which is lost in the mammals. However, he is mistaken in saying (p. 493) that a direct articulation of the ventral part of the atlas with the ventral surface of the basioccipital is lacking in the mammals, for although such an articulation does not occur in the generalized forms, it does occur in some of the specialized, such as Cercoleptes, Gulo, and Taxidea.

General Adaptation of Condyles

The object of the present paper is to point out the types of condyles found among the mammals and to give, so far as possible, the adaptive significance of the several types.

Some 2500 skulls belonging to the American Museum of Natural History and to Columbia University have been examined, and I wish to thank Professor Osborn for his help and suggestions which he has so willingly given.

The occipital condyles are very important, since it is by them that the head articulates with the neck. The head can usually be moved freely in all directions, and in some animals is frequently subjected to great strains, and in order that it may not be dislocated

easily the condyles have become modified in various ways. After giving the various modifications I will attempt to correlate the different types with the habits of the animals, giving, so far as possible, a mechanical explanation for the unusual forms.

They can only be understood in connection with (1) the atlas and axis and (2) the musculature of the occiput and neck. There is a mechanical balance of the ligaments and opposing muscles so that the head is held, with the least amount of effort, in its normal resting position.

The degree of mobility is directly correlated with the curvature of the condyles, and to some extent with their sessile or pedunculate position (Fig. 12, *a* and *d*). The sessile condition never occurs except when the neck is short. When the head can be turned through a large arc the condyles are strongly curved and pedunculate. This is beautifully shown in the birds, in which the single median condyle is pedunculate and hemispherical, an arrangement that permits free motion in all directions. Fig. 12, *e*, shows a sagittal section through a hawk's condyle and *f* a transverse section. The transverse diameter of the two condyles together is always greater in the mammals than the fore-and-aft diameter.

There are three ways of moving the head: up and down, sideways, and in a torsional or twisting manner. Among the mammals, the movement up and down occurs mostly between the atlas and the skull. The torsional movement is mainly between the atlas and the axis, the odontoid process acting as a pivot around which the atlas revolves. To move the head sideways all the cervical vertebræ come into play.

Transition between Monocondylic and Polycondylic Conditions

The monocondylic tripartite and dicondylic conditions are well illustrated in Osborn's paper (:00), the dicondylic condition being derived from the monocondylic by the reduction of the median element.

But reduction does not always occur in the median plane. In some specimens of Gulo the condition is monocondylic (Fig. 4), while in others reduction has taken place, not in the median plane,

but at some distance each side of it, producing a tricondylic condition. This third condyle (Fig. 6, *b*), articulates with the basal part of the atlas when the head is bent downwards sharply, and may be known as the "median condyle." In many mammals the odontoid process is long and when the head is thus sharply bent upon the neck, the process comes in contact with the basioccipital producing a facet (Fig. 6, *a*), which we will call the "odontoid condyle." In the sea otter, *Latax lutris* (Fig. 7), the odontoid and median condyles have each been divided by a depression thus producing *four accessory condyles* or six altogether!

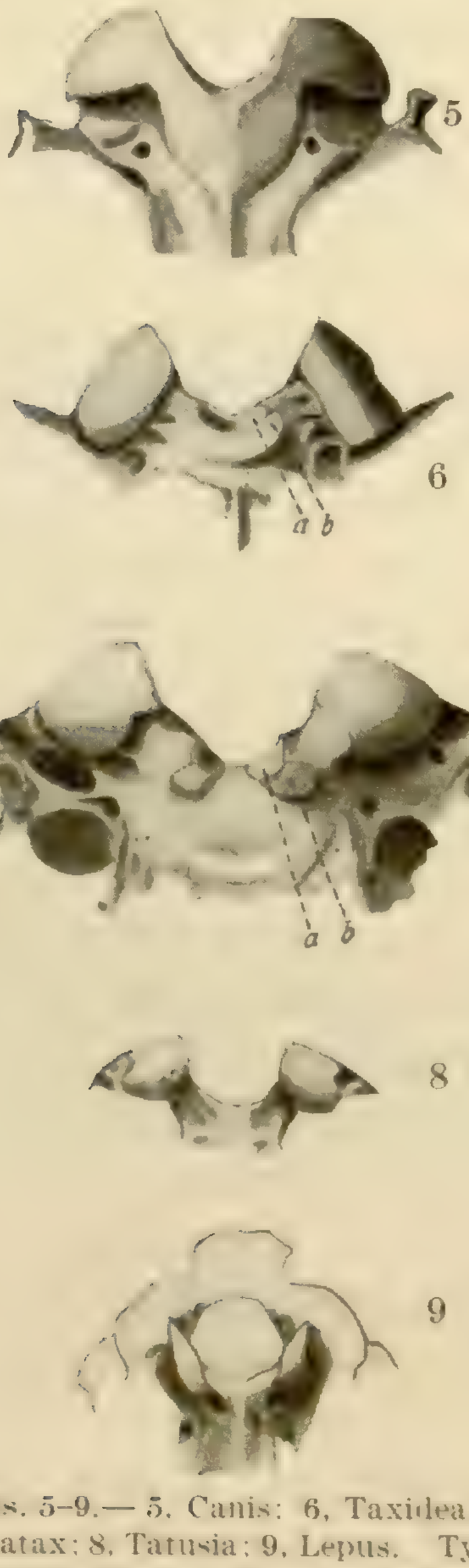
FIGS. 1–4.— 1, Echidna; 2, Putorius; 3, Cercoleptes; 4, Gulo. Types with a continuous tripartite condyle. Gulo shows the condyles prolonged forward, giving a large area of articulation. All ¾ natural size.

This is a process of reduction, the articular faces increasing in number but decreasing in total area, possibly to be correlated with the manner of feeding and the character of the food, principally shell fish, the head and neck losing some of their mobility and not being subjected to such great strains as in the more carnivorous forms. It is only comparatively recently that they have adopted their present habits, and so the reduction of the median condylar area has not been carried to the point of obliteration, since the atrophy of an organ always is slower than its development.

Thus we may look upon the condyles of such a form as Erinaceus as representing a generalized type. Here they are separated by an interval equal to one half the diameter of one of them, they are uniformly curved throughout and not prolonged forward, nor are they noticeably sessile or pedunculate.

Adaptation to Carnivorous Habits

As the animal became more carnivorous in its diet, capturing larger animals, the condyles became larger and stronger, extended forward, became approximated, and finally fused, forming a type with a large condylar area (Figs. 4 and 5). Later, as the animal gave up its habit of capturing large prey and took to feeding on smaller animals, the condylar area suffered reduction, since such strong condyles were not needed, the reduction occurring first at each side of the median line (Fig. 6), and later in the sagittal plane (Fig. 7).



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Figs. 5–9.— 5, Canis; 6, Taxidea; 7, Latax; 8, Tatusia; 9, Lepus. Types with divided condyles. *a*, odontoid condyle; *b*, median occipital condyle. All ¼ natural size.

Thus we get a type with the lateral condyles widely separated and poorly adapted for fighting. If, from the generalized type, the animals have adopted habits requiring little or no fighting, and feeding habits requiring no great development of the neck muscles for pulling and tearing, the condyles never acquire a large articulating area, but remain small and tend to become further separated from each other, as in Homo and Tatusia. In both of these, the ancestral forms have the condyles approaching an Erinaceus-like type.

In the early ungulates (Pantolambda, Phenacodus, Hyrachyus, etc.) the condyles are of a generalized type, while in some of the later forms (Ovis, Camelus, Equus) they are highly specialized, being large, and having a peculiar shape. This has probably been brought about by their

manner of fighting among themselves, and will be discussed farther on.

The position of the head upon the neck has a great deal to do with the direction in which the condyles point, whether straight backward, as in the cetaceans, or downward as in man.

ARRANGEMENT OF CONDYLES IN DIFFERENT ORDERS

Monotremata.—The condyles are very thick and rounded (Fig. 1). The odontoid process is long and has a broad basioccipital facet, which, at the sides, may or may not be confluent with the lateral condyles, this being an individual variation.

Marsupialia.—The condyles are, as a rule, pedunculate and strongly convex, and often widely separated. In Didelphys and Dasyurus there is a slight tendency to bridge over the basioccipital, while an odontoid facet occurs in a few.

Insectivora.—In the burrowing forms, Scapanus, Scalops, and Talpa, the neck is very short and the condyles large and sessile, and extended slightly forward, due to the sessile condition and relatively large size. The odontoid process is long, articulating with the basioccipital. In the less specialized forms, such as Erinaceus, the condyles represent a very generalized type.

Cheiroptera.—All the bats have the condyles separated; usually widely so in the Microcheiroptera, where they are sessile. In those forms that carry the head at right angles to the vertebral axis, the condyles point downward, as in man, while in the large Pteropus, they are directed backward.

Edentata.—All the living Xenarthra have the condyles very widely separated (Fig. 8), but in Metacheiromys, an armadillo from the middle Eocene, they are nearly in contact ventrally.

Rodentia.—Various conditions are met with among the rodents but none worthy of note except that in Lepus. In this form (Fig. 9), the condyles are not only convex dorso-ventrally, but also transversely, their long axes being directed upward and outward.

Carnivora.—The carnivores very often worry their prey, shaking their heads from side to side, and after it is dead, tearing the flesh from the body. In this latter process the head is sharply flexed upon the neck, so that any further ventral motion is stopped

by the ventral portion of the atlas coming in contact with the median condyle or with the anterior prolongation of the lateral condyles, and, since strong ligaments prevent any dorso-ventral motion between the atlas and the axis, any further strain in this direction will be thrown back upon the other cervical vertebræ, where the processes and muscles are stronger and there is no danger of dislocation. The anterior prolongation of the lateral condyles occurs only in the more strictly carnivorous forms. The median condyle and its separation from the lateral condyles is well shown in the Mustelidæ (Figs. 2–4, 6, and 7). The lateral condyles are usually prolonged forward in the Canidæ and Hyænidæ, and these, together with the Mustelidæ, feed in a standing position, not in a crouching position as do the others.

10

11

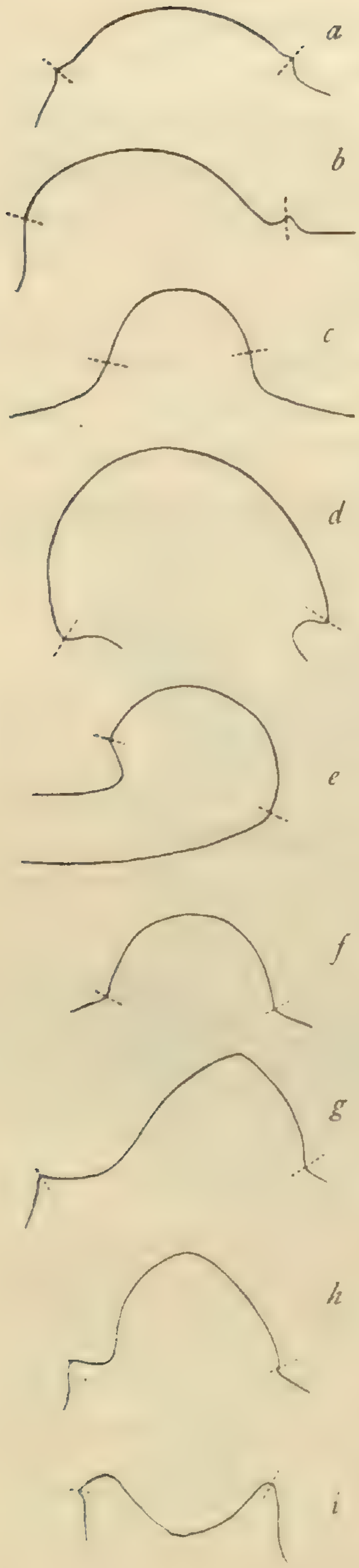
FIGS. 10–11. — 10. Camelus: 11. Ovis. Ungulate types with the condyles prolonged forward. Both ½ natural size.

Cetacea.— All have short necks with a tendency for the cervicals to fuse. The condyles face directly backwards. In all recent forms examined the condyles were sessile and only slightly convex (Fig. 12, *a*). In the Miocene forms (Argyrocetus, Hypocetus, etc.) the condyles were somewhat pedunculate and strongly convex; they had long flexible necks and the head was easily turned, as contrasted with the living cetaceans.

None of the ungulates has a median condyle, nor an odontoid facet upon the skull, nor are the condyles ever confluent ventrally.

Perissodactyla.— The horses always have the condyles prolonged forward, and they are sometimes slightly concave anteroposteriorly at their forward ends.

Correlated with the downward extension of the condyles is the folding over of the condylar articular surface of the atlas onto its anterior face. The tapirs parallel the horses. Neither the titanotheres nor the rhinoceroses have the condyles prolonged forward.



Artiodactyla.— All the horned ruminants have the condyles extended forward and broadened out and curved downward at their anterior ends. Correlated with this, as in the horses, the articular surface of the atlas is extended downward on its anterior face. In fighting, the head is bent downward so that the points of the horns will project forward towards the foe. In this position the head interlocks with the atlas so that when the two animals come together with a rush, there can be no dislocation.

The atlas and axis are firmly bound together by ligaments, so that the force of the impact is thrown back upon the body and posterior cervicals where there is no danger of a dislocation as there is no sharp flexion. Fig. 12, *h* and *i*, cross sections of the condyle and atlas of the aoudad (*Ovis tragelaphus*), shows how the two are reciprocally curved at their ventral ends. The dotted line of Fig. 11 shows where section *h* was taken. A similar condition occurs in the hornless females and in the camels and horses. The females of the horned forms have probably inherited this peculiarity from the males; no reason is known for its occurrence in the camels and horses.

Primates.— In the lemurs the condyles point backward while in the Anthropoidea

FIG. 12.— *a*, Monodon; *b*, Homo; *c*, Dasyurus; *d*, Rhinoceros; *e*, Archibuteo, sagittal section; *f*, transverse section of same; *g*, Camelus; *h*, *Ovis tragelaphus*; *i*, section through atlas of same. Sections through the left condyle from the median aspect showing the antero-ventral portion to the left and the postero-dorsal to the right. The dotted lines in Figs. 10 and 11 show where sections *g* and *h* were taken. Fig. 12, *i*, a section through the atlas that would be opposite section *h* in its natural position, shows how the condylar articular surface is curved over onto its anterior face. All drawn the same size for comparison.

they are usually placed under the cranium and directed downward. They are always widely separated, except in some of the lemurs. Occasionally the odontoid process articulates with the skull (Homo, Cercocebus, some lemurs); no median condyle occurs. On the median part of the condyles there is usually a depression, which in some forms becomes a sharp notch.

In some of the mammals (Hyæna, Tragulus, Equus, Ovis, Camelus, Figs. 10, 11, and 12, *g*), the articular surface of the condyles, instead of having a continuous curve, possesses a ridge running obliquely outward and upward from about the middle of the inner border of the condyles. No explanation is offered for this peculiar condition as it apparently reduces the efficiency of the condylar articulation. The habitual position of carrying the head, and its direction with reference to that of the atlas, will probably offer some explanation.

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LIVING AND FOSSIL SPECIES OF COMPTONIA

EDWARD W. BERRY

Introduction

When we find a genus which is monotypic in the existing flora, or one which contains but two or three geographically remote species, we may rest assured that the genus in question had an interesting geological history, and that its living representatives are relicts of a day when the genus was widespread and dominant. Notable examples, such as Liriodendron, Sequoia, and Nelumbo, may be cited. Comptonia is no exception to this rule. The single living species is confined to eastern North America, ranging as a low shrub from Nova Scotia to Manitoba and southward to North Carolina, Indiana, and Tennessee, while the number of ancient forms that have been described, is upwards of three score and amply proves the cosmopolitan character of the genus during the Tertiary period.

Recent paleobotanists refer them as a subgenus to Myrica, as is done in case of the living species by Engler (*Natürlichen Pflanzenfamilien*, vol. 2, pt. 1, p. 28, 1889). Modern usage in this country, however, gives Comptonia generic rank, quite rightly so it seems to me.

The space of a generation has passed since Schimper's classic *Traité de Paléontologie Végétale* sought to unify paleobotany, and the chaos of described species is even greater to-day than it was previous to 1870. Paleobotany is surely far enough advanced, it seems to me, for a more philosophical treatment, and while this little essay makes no pretension at embodying such a treatment, it is hoped that it will furnish the material that will be useful for that purpose when the proper time arrives.

It is obvious enough to most botanists that existing species vary in their leaf characters through very wide limits. I have had considerable to say about the leaf variation, atavistic and otherwise,

of Liriodendron and Sassafras, and the same variability is true of that most interesting relic of bygone days, the Ginkgo; while numerous instances of similar variations in other genera could be cited. For a number of years I have been engaged in collecting leaf specimens to illustrate this variability in a number of genera, and I find this task to be a never-ending source of interest in addition to the invaluable data which it furnishes for the understanding of earlier floras.

If it be objected that the consideration of geographically widely removed forms as identical leads only to confusion, the answer is —a consideration of the variability in the living Comptonia, the unmistakable proof in its present and past distribution of its wide range, coupled with the tendency to call a certain form by a certain name because it is like a form perhaps wrongly named by Brongniart or Heer or Lesquereux, without a very serious consideration of the generic affinities, in fact it can scarcely be said that we have any generic limits in a host of Mesozoic and Neozoic genera; all these tend to discredit specific distinction based on geographical remoteness.

These considerations lead me to think that the present is not an inopportune time for an attempt to work out the relations of such forms as may be referred to Comptonia, and to see if even a little light cannot be shed on their history. And at the same time to reduce the number of species (so called), often based as they are upon irrecognizable fragments. Surely several score of species, some entirely inadequate, leave room for more confusion than slight errors in the opposite direction. The forms here considered as identical all show such slight variations as would not be considered for a moment were we dealing with leaves in the existing flora.

THE SUCCESSION OF FORMS

Comptonia branched from the Myrica stock, most probably during the lower Cretaceous. Its original home was in all probability in the greatly extended lands of the semitropical or warm temperate Arctic region, although the earliest known speci-

men from that region is from the Cenomanian of Greenland (Atane beds). One of the first floral migrations southward during the Mesozoic was along the Atlantic coastal plain, which at that time was possibly continuous along the northeastern coast of America from Greenland south. Traces of this ancient coastal plain are said to have been found off the present New England coast, and the difficulties of accounting for the remarkable similarities in the Cretaceous flora of Greenland and that of the Atlantic coastal plain seem insurmountable unless we predicate some sort of a direct land connection, so that floral distribution tends to furnish support to Suess's theory as to the origin of the Atlantic ocean.

The Myricas were a prominent element in this Mesozoic migration, a single species being recorded from the lowermost Cretaceous of Virginia. In strata of approximately Albian age (Raritan, etc.) there are ten species of Myrica, and at this time occurs the earliest known Comptonia, in the Raritan of New Jersey.

The resemblance of this and other primitive Comptonia leaves to those juvenile and atavistic leaves of the modern species is discussed in a later portion of this paper.

That Comptonia is derived from Myrica, aside from the morphological and other evidence furnished by a study of existing species, seems probable (1) from the fact that it originated among an abundant display of Myrica species some of which preceded it in time, (2) from its progressive increase in the number of species and in their ever widening distribution up to the close of the Miocene, paralleling a like history for the genus Myrica, (3) the numerous leaf remains that have been found intermediate in character between Myrica and Comptonia, (4) the resemblance to Myrica of the oldest Comptonias and of the leaves of modern seedlings.

As an example of the variation in Myrica leaves and their tendency to approach the Comptonia form, I may cite *Myrica lignitum* Unger, an undoubted Myrica, abundant in the Oligocene and Miocene of Europe. Ettingshausen and Standfest[1] in their study of the abundant remains of these leaves from the late Tertiary of

[1] Ettingshausen und Standfest. "Ueber *Myrica lignitum* Ung., und ihre Beziehungen zu den lebenden Myrica Arten." *Denkschr. math.-natur. Akad. Wiss. Wien*, vol. 54, pp. 1–8, pls. 1, 2, 1888.

Styria, recognize thirty varieties of which several are very close to Comptonia, in fact were it not for the closely related intermediate forms as well as the characteristic Myrica fruit, we would be justified in considering them as referable to Comptonia.

Contemporaneous with the southward advance of Comptonia in eastern North America, we find a like advance through northern Europe *via* the then extended Scandinavian peninsula, recorded by a primitive species of Comptonia (*antiqua* Nilss.) from the greensand of Köpinge, Sweden, followed by the appearance of the same species in Transylvania (Cenomanian). This species is very close to its American and Arctic congeners, so similar that one cannot but see in these leaves the strongest sort of an argument for a common ancestry, a theory which receives additional strength, not only from the form of the juvenile leaves of the existing species, but also from the fact that there is nothing in our present knowledge of floral distribution in past time or of the disposition of the land masses of the northern hemisphere during the Mesozoic that does other than add support to such a theory.

Some authors (*e. g.*, Hosius and von der Marck) would include *Dryandra cretacea* of Velenovsky from the Cenomanian of Bohemia in this genus. While it is true that the form and venation of the leaves is the same as that characterizing the leaves of certain Miocene species of Comptonia, and that with the aid of mutation (as used by deVries, not Osborn) there would be no difficulty in deriving this species from the contemporaneous Myrica stock, especially when we note that we have no evidence that in habit and structure it differed from the contemporaneous Myricas, the only difference about which we know anything is the difference in leaf-form, and the evolution of leaf-form is a comparatively simple affair. Still I think that the inordinate length of these specialized leaves, combined with the character of the marginal serrations, together with their geological position, renders it probable that Dryandra is a more reasonable index of their real botanical relations. I certainly do not feel that the evidence is sufficient for making the change in generic affinity suggested.

The upper Cretaceous history of Comptonia is a blank in so far as America is concerned. In Europe, however, we find a characteristic Comptonia (*tenera* Hos. & v. d. Marck) in the Senonian

of Westphalia. This species shows a considerable progression from the earlier Cretaceous form, and clearly foreshadows the later type of leaf, so abundant in the Tertiary floras, and which is not very different from the typical modern leaf.

With the ushering in of the Eocene, we find this type of leaf continued in considerable abundance and showing more or less variability in the direction of other species. The European records of this age are far superior to those of America; while the Arctic region unfortunately has thus far furnished no evidence (except for the single leaf which I have referred to *Comptonia microphylla* and whose age is doubtful).

The Atlantic coastal plain, where we would expect to have found a most interesting group of species, had the records only been preserved, fails us entirely, as no leaf beds have been found in their marine formations. Western America it is true furnishes us with Eocene Comptonias, but these are relics of an independent line of migration from the Arctic region during which three species occurred in Alaska. These either represent the genus *en route* for Asia, or are stragglers which were left behind during the Asiatic advance. The Green River beds, besides some fragmentary remains, furnish us with a beautiful species, which we picture as a prominent element in the flora that clothed the site of the present Rocky Mountain region.

Asia has thus far failed to show Comptonias in strata earlier than the Miocene, due no doubt to our lack of knowledge of earlier Tertiary formations and floras in that region. As previously mentioned it is in Europe that we find the most satisfactory evidence of Comptonia development.

Beginning with the same type of leaf as that of the Senonian *tenera*, which is common during the Eocene as *Comptonia schrankii*, and which becomes widespread, we find various lines of variation leading to the closely related and equally abundant *Comptonia diforme*, and to the less common forms which I have shown in the genealogical diagram.

We find at this time the modern type of leaf and the same variations from this type, *i. e.*, small leaves, large leaves, leaves with acute lobes, and leaves with obtuse or rounded lobes; in all, some twelve forms which appear to be valid species.

The next period, the Oligocene, shows a considerable broadening out in their development and distribution. From the *vindobonensis* type we get, by a series of slight gradations, *Comptonia œningensis*, and by equally slight steps this type gives rise to that most beautiful species, *Comptonia laciniata* with its large leaves and serrated lobes. This form is strongly suggested in the leaves of the modern species. The small-leaved types of *schrankii* and *diforme* continue through this period, and near them we have the large and handsome form, *Comptonia dryandroides*, so like the modern leaf, besides two or three other species of more doubtful value — in all twelve species.

It is in the next period, however, the Miocene, that the genus reaches its acme of development. Numerous leaf remains, often beautifully preserved, are present at nearly every locality where plant beds of this age have been opened, from Greece and Bohemia to France and the Baltic. We find a continuation and further development of all of the Oligocene types, the small *schrankii* with both rounded and acute lobes, the somewhat larger and rather acute-lobed *diforme*, the obtuse-lobed *œningensis* and *vindobonensis*, and the related large-leaved *laciniata* and *dryandroides*, besides numerous other forms, including the gigantic *grandifolia*.

We find *laciniata* getting over into Asia Minor from southeastern Europe. Eastern Asia (Japan) furnishes two good species which are identical with European forms. Northwestern America furnishes two additional forms also identical with European forms, one of them being the same as one of the forms from Japan. Whether we have in these occurrences the evidence of an interchange of species between the continental regions or independent lines of southward migration from the Arctic region is not positively determinable. I incline to the latter assumption, however, which is supported by the evidence of *dryandroides* (*cuspidata* of Daws.) from western Canada which is identical with *naumanni* Nath. from Japan, both in turn identical with the leaves which occur in southeastern Europe from this and earlier horizons. It would seem that the Japanese and Canadian leaves had both traveled southward along the foothills bordering the valleys, which in their general trend run north and south, rather than that they came overland from Europe to Asia then across Behring Straits

and down the western American coast or *vice versa*. In all, we have during the Miocene, forms which may be divided up into nine "good species."

With the refrigeration of Pliocene and Pleistocene climates in temperate latitudes, and the resulting wholesale extinction and redistribution of species, we see Comptonia exterminated from all except American soil. The story is apparently the same for numerous other genera which are exclusively American in the existing flora; the Mediterranean Sea in Europe and the high altitudes of southern Asia apparently cutting off their retreat before the advancing ice sheet.

Comptonia is a hardy shrub at the present time and thrives in almost any habitat, possibly as the result of its struggles with severe conditions during the Glacial period.

Venation

In spite of the considerable variation in leaf-form shown by the leaves of *Comptonia peregrina* (Linn.) Coulter, the venation is monotonously uniform. In a general way it may be characterized as follows: there are two or three secondaries in each lobe, generally two in the smaller lobed forms and three in the larger, although those with two seem to be the commoner irrespective of size. They all branch from the midrib at a wide angle, often 90 degrees, and describe a slight upward curve, which is greater in the lobes toward the tip of the leaf. The uppermost secondary in each lobe usually runs directly to the tip of the lobe when the latter is pointed, or directly to the margin in those leaves with rounded lobes, its position on the margin being indicated by a slight mucronate point. The one or two secondaries below the upper are inserted at equal distances apart and become somewhat more curved as they proceed outward, curving upward to join a short downwardly directed lateral branch from the secondary next above. The tertiary venation in the border region is festooned along the margin of the leaf, being particularly noticeable along the lower margins of the lobes. Where the lobes have a somewhat serrated margin or are divided somewhat similarly to those of

the fossil species *Comptonia laciniata*, this arching of the veins along the border is more or less interfered with, and a branch from the nearest secondary proceeds to the tip of the tooth. Where the lobes are not separated to the midrib there is usually a vein of the same caliber as the secondaries which proceeds directly to the sinus between the lobes, where it forks and its two branches arch along the borders of the adjacent lobes on each side (above and below). The finer areolation shows three-, four-, or five-sided reticulations. On the whole the venation cannot be said to show any especially characteristic and distinctive features. The usual style of leaf is finely figured by Schimper in his *Traité de Paléontologie Végétale*, Plate 84, Fig. 4 (1874), which is copied from a figure of Ettingshausen, in his *Blattskelette der Apetale*.

REVERTED FORM OF SEEDLING LEAVES

In discussing *Comptonia microphylla* I have mentioned the curiously shaped leaves of the seedlings of the existing species, the first six or seven of which are indistinguishable from those of the earliest Comptonias from the Mid-Cretaceous, and which are evidently true reversions. Some of these are well shown on Plate 3. I have collected numerous examples of these leaves and believe this form to be a constant feature of the seedling leaves, furnishing admirable proof of the correct identification of their Cretaceous ancestors.

As might be expected, the various fossil species of Comptonia probably had leaves on their seedlings which were similar to this form. Seedling plants, as can be readily understood, are rare as fossils. I am convinced, however, that the leaves which Heer[1] refers to *Myrica latiloba* from the Miocene of Locle and Oeningen are to be so understood. Their form and venation are exactly that of the modern seedling leaves and they have the same thin texture and thickened midrib. Lesquereux's Fig. 12 of *Myrica alkalina* from the Green River group of Wyoming is also a young leaf, probably of *Comptonia insignis* (Lx.) Berry.

[1] Heer. *Fl. Tert. Helv.*, vol. 3, p. 176, pl. 150, fig. 12–15, 1859.

Stipules

The stipules on the modern plant are large, ordinarily of an odd, three-lobed form, the upper lobe being produced into a horn which runs close to the petiole. These stipules are pronounced in seedlings and spring shoots, no doubt serving as a protection from the cold. They become, however, much reduced in size and abbreviated in form on the later shoots. They are also very variable, some of the extreme forms being shown on Pl. 1, Figs. 8–12, Figs. 11 and 12 being the more typical. As in Liriodendron, they are probably descended from the basal lobes of the leaves of their ancestors, for we find basal lobes in the modern plant which approximate the stipular form and which are entirely separated from the lobes next above. Pl. 1, Figs. 4–7, illustrates some of these basal lobes and serves admirably to show how strikingly they approximate the stipules in appearance.

Compound Leaves

The leaves of the modern species show occasional examples of a tendency toward the formation of compound leaves. Usually it is toward the tip that the midrib forks, forming two lobes. Sometimes, however, a basal lobe will assume the size and proportions of a division of a compound leaf. On Pl. 1, Figs. 1–3, are shown three examples of this tendency. In Figs. 1 and 3 the midrib forks about halfway to the tip, thus forming two divisions of equal rank. In Fig. 2 the tendency seems to be toward a tripalmate division, the central division being bilobed and separated by an interval of petiole (midrib) from the rest of the leaf.

I know of no fossil remains which approach these modern leaf variations.

It has been suggested to me that the leaf variations in the existing species may indicate that this apparently monotypic form may be segregated into a number of closely related species, like so many aggregations of the Asa Gray period. This may be so; it were rash nowadays to doubt the possibilities of any species in this direction after seeing what has happened and is happening to Cratægus

and other genera. However, no evidence in this direction is furnished by the variations in leaf form, for with the exception of the atavistic character of the seedling leaves which appears to be a constant feature, and the usual reduction shown by the senescent leaves, the leaf variation is entirely fortuitous, if one may use that term in this sense for the result of unknown, or at least not well understood morphological and physiological causes.

THE FOSSIL SPECIES

That the number of fossil species of Comptonia has been multiplied beyond what the facts warrant, seems probable without any very serious consideration. That we should have, for instance, in the area of Europe, ten or a dozen Eocene, Oligocene, and Miocene species seems improbable, and this off-hand conclusion is borne out by an examination of the species. We find that the limits of variation within a single species as conceived by the various writers who have studied members of this genus, judging by the diverse forms referred to the same species, are so wide as to include in almost any of the described species (so called), greater differences of size, form, or venation than exist between what are usually regarded as really valid species by the individual authors. In addition we find species founded upon obscure fragments of doubtful value, or upon what are very probably immature or abnormal leaves. More especially does this seem to be the case when we examine the leaves of the sole existing species for comparison. The latter show wide variations (see Pl. 2). The typically mature leaves are usually divided nearly to the midrib, although the sides of the lobes often overlap, giving them the appearance in some cases of being only slightly incised. This would be particularly true of similarly lobed leaves preserved as fossils. The leaves are progressively simpler toward the flowers and in the seedlings, becoming merely serrate or even entire and lanceolate (Pl. 3). Thus the juvenile and senescent leaves are both more or less atavistic. The lobes vary greatly in outline duplicating many of the fossil leaves in appearance; their margins are usually entire but may be incised as in several of the fossil leaves.

On the whole I feel justified in suggesting the changes which

follow, the discussion falling naturally under the respective species. While the synonymy does not pretend to be complete, I have endeavored to include all references to figured specimens and have been at much pains to verify them in so far as the facilities of the United States National Museum and the New York Botanical Garden would permit.

Work of this sort is as laborious as it is unappreciated, indeed the author who has the temerity to break away from the traditional names in paleobotany is more than likely to be criticised for having "done nothing but burden an already overburdened synonymy." I have been working on Comptonia for several years and have long hesitated about publishing my results for just this reason until perfectly convinced that it was entirely impossible to get any idea of the past history of the genus without correlating the various remains, either positively or at least provisionally. To leave them as they were would be about as sensible as it would be to have species of Comptonia in the existing flora based upon the political divisions in which the plants are found and further dependent on the slight variations in leaf-form exhibited by the individual plants. A number of doubtful forms such as *Comptonia contzeniana* Debey, *Comptonia chironis* Massal, *Comptonia heerii* Ettings., etc., and such obvious errors as *Comptonia mirabilis* Brongn. cited in Prestwich's *Geology* are entirely omitted.

Comptonia diforme (Sternb.) Berry

Asplenium diforme Sternb., *Fl. d. Vorwelt*, vol. 2, pp. 29, 33, pl. 24, fig. 1, 1822.

Aspleniopteris difformis Sternb., *Ibid.*, vol. 4, p. 21, 1825.

Zamites difformis Presl. in Sternb., *Ibid.*, vol. 2, p. 198, 1822.

Buettner, *Rudera Diluvii Testes*, pl. 22, fig. 8, 1710.

Pterophyllum difformis Göpp., *Ubersicht. d. Arb.*, p. 137, 1844.

Comptonia acutiloba Brongn., *Prod.*, pp. 141, 143, 209, 1828; *Tabl.*, p. 121, 1849.

Unger, *Synopsis*, pp. 213, 305, 1845; *Gen. et Sp.*, p. 393, 1850; *Foss. Fl. v. Sotzka*, p. 32 (162), pl. 8 (29), figs. 6–8, 1850.

Saporta, *Périd. Végét.*, p. 307, fig. 92; *Mon. d. Pl.*, 1879; *Orig. Pal. Arbes. Cult.*, p. 141, 1888.

Gardner, *Mem. Geol. Surv. Eng. & Wales*, p. 108, 1889.

Boulay, "Fl. foss. Gergovie," *Ann. Sci. Brux.*, vol. 23, p. 73, 1899.

Dryandra acutiloba (Brongn.) Ettings., *Proteac. d. Vorw.*, p. 27 (735), pl. 4 (33), figs. 2, 3, 1851; *Foss. Fl. v. Bilin*, vol. 2, p. 17, pl. 35, figs. 18–26, 1868; *Proc. Roy. Soc. Lond.*, vol. 30, p. 232, 1880.

Myrica (*Comptonia*) *acutiloba* Brongn.
Schimp., *Pal. Végét.*, vol. 2, p. 560, 1872.
Engelhardt, *Nova Act. Leop. Carol.*, vol. 39, p. 375, pl. 23, figs. 7–12, 1877; *Ibid.* vol. 57, p. 153, pl. 6, figs. 4–7, 1891; *Sitzb. naturwiss. Gesell. Isis*, 1880, p. 78, pl. 1, figs. 6, 7, 1881; *Lotos*, neue folge, Bd. 16, p. 5, 1896.
Heer, *Fl. Foss. Arct.*, vol. 7, p. 77, 1883.

Dryandra comptoniæfolia Ettings., *Beitr. z. kr. foss. Fl. Neuseelands*, p. 27, pl. 4, figs. 14–18a; pl. 5, figs. 9–12, 1887.

Comptonia columbiana Daws., *Trans. Roy. Soc. Can.*, vol. 8, sec. 4, p. 81, fig. 10 (text), 1890.

Comptonia Vinayi Saporta, *Pl. foss. Ark. de Brives*, p. 35, pl. 3, figs. 9–13, 1878.

Dryandra saxonica Friedrich, *Abh. geol. Specialk. Preuss u. Thüring.*, vol. 4, pp. 327, 382, pl. 20, figs. 10a–16; pl. 28, figs. 3–5; pl. 29, fig. 16, 1883.

This was one of the first known species of Comptonia, having been described and figured by Sternberg in 1822 under the name *Asplenium diforme*. What is probably the same thing is mentioned elsewhere in his *Flora der Vorwelt* as *Aspleniopteris difformis* Sternb. and *Zamites difformis* Presl. A similar leaf was figured by Buettner as long ago as 1710 and considered as having Cycadean relationships.

We have in this species, or group of species of the *acutiloba* type, a widespread and persistent type of leaf which is fairly well marked. Some of the smaller specimens, it is true, resemble *Comptonia schrankii*, particularly Ettingshausen's forms from Monte Promina, but the bulk of the leaves referred to the latter species are smaller and have very narrow, two-veined, acute lobes. Heer includes under *Comptonia acutiloba* the *Comptonia incisa* of Ludwig found at several localities in Hesse, and he also identifies a similar leaf from Greenland as *Comptonia incisa*. The Greenland leaf is identical with Ludwig's leaves, but both are obviously distinct from *C. acutiloba*.

Dawson's form from British Columbia belongs here. He says that it is closely allied to *Comptonia matheroniana* Sap., but I fail to see any resemblance to that species. Species which do resemble

Dawson's more or less, are *Comptoniphyllum japonicum* Nath., and especial'y *Comptonia partita* Lesq., the latter based upon a poorly drawn fragment from the Green River beds.

The existing Comptonia sometimes furnishes leaves very similar to *diforme*, and I have collected many such, although usually they differ in being somewhat broader, *e. g.*, Pl. 2, Fig. 4.

The many excellent figures published by Ettingshausen furnish adequate and typical examples of the leaves of the species under discussion. This form of leaf makes its appearance during the Eocene at the widely separated localities of the Isle of Wight in England, Brives in France (represented by *C. vinayi* Sap.), and Murderer's Creek in New Zealand. It is possible that the New Zealand leaf, which is identical in form, may have been borne on an entirely different plant, as it is difficult to account for so wide a distribution. It may well be that the New Zealand leaf should be referred to Dryandra as Ettingshausen has done, since several species of the latter genus have been recorded from that region by the same author, all having leaves of the *acutiloba* type. In discussions of the distribution of Comptonia we should constantly bear in mind, however, the meagerness of the record of the upper Cretaceous period.

Comptonia diforme continued through the Oligocene and Miocene, becoming common during the latter age and occurring in beds in this country which have been considered Miocene (*Comptonia columbiana* Daws.).

Friedrich considers the Saxon leaves which he describes under the name of *Dryandra saxonica* to belong to that genus because of their acute lobes, subcoriaceous texture, and style of venation, in which characters he says they differ from the modern Comptonia leaf. If he had seen a large enough series of the latter he would have found no difficulty in recognizing their similarity and the fact of their identity with both fossil forms whose similarity he does note, *i. e.*, *schrankii* and *acutiloba*, all of which I have included under *Comptonia diforme.*

Comptonia gaudinii Heer

Myrica (*Comptonia*) *gaudinii* Heer, *Fl. Tert. Helv.*, vol. 2, p. 34, pl. 70, fig. 9, 1856; *Ibid.*, vol. 3, pl. 152, fig. 19, 1859.
Schimp., *Pal. Végét.*, vol. 2, p. 559, 1872.

Comptonia incisa Ludwig, *Palæont.*, vol. 8, p. 96, pl. 30, fig. 7–15, 1860.
Heer, *Fl. Foss. Arct.*, vol. 2, p. 474, pl. 39, fig. 7, 1871 (referred to *Dryandra acutiloba* (Brongn.) Ettings).
Schimp., *loc. cit.*, p. 561.
Comptonia triangulata Watelet, *Pl. Foss. Bass. Paris*, p. 124, pl. 33, fig. 4, 1866.
Myrica credneri Engelh., *Nova Act. Leop. Carol.*, vol. 39, p. 376, pl. 23. fig. 13, 1877.
Myrica (*Comptonia*) *tschernowitziana* Engelh., *Ibid.*, p. 375, pl. 23, fig. 14.
Comptoniphyllum japonicum Nath., *Pal. Abh. D. & K.*, vol. 4, pp. 207, 212, pl. 20, figs. 2, 3; pl. 22, fig. 3, 1888.

This species embraces leaves approaching the *acutiloba* type, averaging, however, considerably larger in size. They are similar to *Comptonia dryandroides* Ung. except that the lobes in the latter species are fewer in number and more falcate in outline. As will be seen from the foregoing synonymy I have included a variety of names under this species, most of them having been based upon fragmentary material. Some of these may be entitled to varietal rank, but surely their slight differences do not entitle them to rank as valid species. For instance, Engelhardt's *tschernowitziana* is based upon a single specimen showing but three lobes on one side and one lobe on the other side. It differs from the typical *gaudinii* in the more rounded upper margins of the lobes, but might easily be a larger leaf of the same author's *credneri*, both of which I include under *Comptonia gaudinii*. Individual lobes of Ludwig's *incisa* which correspond with *tschernowitziana* could be selected without much difficulty. Heer's *gaudinii* was founded upon fragments as was also the Arctic form which he refers to *Dryandra acutiloba*, but which seems to belong here. His comparison of *gaudinii* to *dryandroides* Ung. is certainly significant. Watelet's *triangulata* is another fragment showing only three complete lobes on each side. Schimper includes it under Watelet's *concisa* from which it manifestly differs, however. Nathorst's *japonicum* shows only the central portions of several large and small leaves. As might be expected when dealing with fragments, the various authors compare their specimens with a variety of other species, for instance Engelhardt compares *credneri* with *macroloba* of Wessel & Weber, to which I fail to detect any resemblance.

Comptonia gaudinii as here constituted, shows considerable range, being represented as early as the Eocene by the leaf described by Watelet which grew on the shores of the Suessonien Gulf, and continued as late as the Miocene of Switzerland and Japan.

Comptonia insignis (Lesq.) Berry

Myrica insignis Lesq., *Ann. Rep. U. S. Geol. & Geog. Surv. Terr., for 1874*, p., 312, 1876; *Tertiary Fl.*, p. 135, pl. 65, figs. 7, 8, 1878.
Myrica alkalina Lesq., *Cret. & Tert. Fl.*, p. 149, pl. 45A, figs. 10–15, 1883.

I regard these two species of Lesquereux as most probably identical, for example his Figs. 13 and 15 of *alkalina* are particularly close to *insignis*, especially Fig. 15. It would require but a slight increase in the lobation of the latter to produce the typical *insignis*. Other than this the remains of the two forms are exactly alike in texture and venation, except that in *insignis* the midrib is more slender. As Lesquereux remarks, the leaves which he refers to *alkalina* are of two types—obtuse, and acute-lobed,—the collected specimens, however, showing every gradation between these extremes, some leaves being acutely lobed on one side and obtusely on the other. As the remains are all from strata of the same age, although Alkali Station, Wyo., is some 300 miles distant from Florissant, Col., I am still inclined to think that the leaves which Lesquereux called *alkalina* are simply the young leaves of which *insignis* is the mature leaf, for they are (1) much more variable in lobation, (2) smaller in size and definiteness, and in the extent of their lobes, combined with a narrower lamina, and (3) they have a much thicker midrib. This is especially true of Fig. 15 cited above.

All of these are characters which serve to mark the leaves of the immature plants of the existing species. Together these two types of leaf show that a most beautiful species of rather broad-leaved Comptonia dwelt on the site of the present Rocky Mountains during the early Tertiary.

The venation which is well preserved, shows a type which is quite characteristic of the modern Comptonia leaf.

Lesquereux compares *alkalina* with *Myrica vindobonensis* Ettings. and with *Myrica ungeri* Herr (*laciniata* Ung.) to both of which there is a passing resemblance that is by no means close, however.

Comptonia macroloba (Web. & Wess.) Berry

Dryandra macroloba Web. & Wess., *Palæont.*, vol. 4, p. 147, pl. 25, fig. 11, 1856.
Myrica macroloba (Web. & Wess.) Schimp., *Pal. Végét.*, vol. 2, p. 557, 1872.
Comptonia concisa Watelet, *Pl. Foss. Bass. Paris*, p. 123, pl. 33, fig. l, 1866.
Myrica concisa (Wat.) Schimp., *Pal. Végét.*, vol. 2, p. 554, 1872.

These leaves resemble those which have been described and figured by the respective authors as *incisa* Ludw. (*gaudinii* Heer), *dryandroides* Ung., and *acutiloba* (*diforme* (Sternb.) Brongn.), with this difference that the blade in *macroloba* is incised only half the distance to the midrib, surely not a very important character in view of the variation in this direction often shown by the existing Comptonia.

Watelet's leaf is not different, except in the foregoing particular from the fragment which he named *Comptonia triangulata* and which I have referred to *Comptonia gaudinii* Heer.

Both of the forms which I have united to form the species under consideration are fragments of the basal portions of single specimens and possibly their similarity may be due to this fact. Neither has any individual characters of much specific weight and perhaps it would be wiser to discard them altogether or to refer them to some of the above mentioned and better characterized species. The French specimen is from the lower Eocene while the Prussian is from the later Tertiary (Aquitanian), which may be considered an objection to considering them identical. However, they are of no great importance in any event, and do not throw any additional light upon the evolution of the genus in Tertiary times.

Comptonia antiqua Nilsson

Phyllites (*Comptonia? antiqua*) Nilss., *Vetens. Akad. Handl.*, for 1831, p. 346, pl. 1, fig. 8, 1832.
Sap., *Arch. Sci. Phys. & Nat.*, vol. 28, p. 110, 1867.
Comptonites ? antiquus Nilss., *Pfl. Kreidegebirges*, p. 121.
Hisinger, *Lethæa Suec.*, p. 111, pl. 34, fig. 7, 1837.
Unger, *Synopsis*, p. 213, 1845; *Gen. et Sp.*, p. 395, 1850; *Sitzb. Akad. Wiss. Wien*, vol. 51, p. 379, 1865.
Brongn., *Tabl.*, p. 111, 1849.
Dryandra antiqua Ettings., *Proteac. d. Vorwelt*, p. 31 (739), 1851.

During the time that *Comptonia microphylla* Heer was spreading southward along the Atlantic coastal plain in America, a very similarly leaved plant had reached Europe by way of the Scandinavian peninsula. This species is represented by the leaf which Nilsson described in 1832 from the Greensand of Köpinge, Sweden. That this species became more widespread in Europe than the fossils which have been discovered show, is indicated by its occurrence at almost the opposite end of Europe in the Cenomanian at Déva, Transylvania.

It was a small leaf with a few rounded lobes and was very similar in appearance to its Arctic and American congeners. In size and outline it is identical with Heer's type figures of *Comptonia parvula* and *microphylla*, particularly the latter, while his Fig. 3 of the former is indistinguishable from the European leaf. Newberry's leaf from New Jersey is larger and has somewhat more pointed lobes, and Heer's *parviflora* is also somewhat larger.

The occurrence of this same type of leaf on the seedlings of the modern plant, and as the earliest known Comptonia leaves in the Cretaceous of such geographically remote localities in Europe, Greenland, and New Jersey, amounts to a demonstration, it seems to me, that we are dealing with an ancestral form of Comptonia leaf, and as a corollary, that the juvenile leaf-forms in the modern plant are truly atavistic.

Comptonia tenera Hos. & v. d. Marck

Comptonia tenera Hos. & v. d. Marck, *Palæont.*, vol. 31, p. 227 (3), pl. 19 (1), figs. 3, 4, 1885.

The next occurrence of Comptonia in Europe after that of *Comptonia antiqua* Nilss, of the mid-Cretaceous, is this species, which Hosius and von der Marck found in the upper Senonian of Westphalia at Höpingen, three and one half miles west of Münster. They compare it to *Myrica dryandræfolia* Brong. (*Comptonia schrankii*) and consider the resemblance to be very close. They also make comparisons with *Dryandra cretacea* Velen., which they think is identical with *Dryandra brongniarti* Ettings. from Häring, both of which species they would refer to the genus Comptonia.

The venation of *Comptonia tenera* is not shown in the speci-

mens figured but there can be no doubt of its being a Comptonia. A large number of the smaller leaves of the existing species are counterparts of these Senonian forms, the most similar figured specimen being the leaf shown on Pl. 2, Fig. 1.

This species differs decidedly from *Dryandra cretacea* Velen., which I would retain in the Proteaceæ, otherwise the authors comparisons are most fortunate and it is very probable that we have in *Comptonia tenera* the Cretaceous ancestor of *Comptonia schrankii* which is so common from the Eocene through the Miocene.

Comptonia dryandroides Unger

Comptonia dryandroides Unger, *Foss. Fl. v. Sotzka*, p. 31 (161), pl. 6(27), fig. 1, 1850.
Andrä, *Jahrb. k. k. geol. Anst.*, vol. 5, p. 562, 1854.
Dryandra ungeri Ettings., *Proteac. d. Vorwelt*, p. 30 (738), pl. 4, fig. 1, 1851.
Unger, *Foss. Fl. v. Kumi*, vol. 35 (59), pl. 9, fig. 16–18, 1867.
Myrica (*Comptonia*) *dryandroides* Pilar, *Acta Acad. Sci. Slav. Merid.*, vol. 1, p. 31, pl. 13, fig. 18, 1883.
Comptoniphyllum naumanni Nath., *Pal. Abhandl. D. & K.*, vol. 4, p. 8, pl. 2, fig. 2, 1888.
Myrica (*Comptonia*) *cuspidata* (Lesq.) Dawson, *Trans. Roy. Soc. Can.*, vol. 8, sec. 4, p. 80, fig. 9, 1890.

A large-leaved and beautiful species of which Unger has figured a perfect leaf from Sotzka, which is identical with, but somewhat larger than Nathorst's *Comptoniphyllum naumanni* from Japan. These leaves are practically the counterparts of numerous leaves of the existing species (*cf.* Pl. 2, Figs. 3, 4). Those which are described by Unger from Kumi have a prolonged base, which the other included leaves lack. This is, however, a variable feature, often present, though in a somewhat less degree, in the existing species. Ettingshausen refers these leaves to Dryandra making comparisons with *Dryandra armata* R. Br. of the existing flora. His comparison is not, however, particularly fortunate as the latter species has leaves which incline to a runcinate form, while the basal portion of the leaf is much more narrowly lobed, some of the lobes being several times longer than they are wide and separated by an

interval of midrib. I altogether fail to see any but the most general resemblances.

With regard to the relations of *Comptonia dryandroides* to the other fossil species of Comptonia the following points may be mentioned.

The lobes are of the form of *schrankii* but much larger and the leaves as a whole are comparatively less elongated. There is somewhat of a resemblance to the typical *acutiloba* leaves but the size is greater and the lobes are longer and incurved. The leaves of *œningensis* have similar lobes when they are deeply lobed, but the leaf as a whole is smaller and the incisions never seem to reach the midrib as they do in *dryandroides*. Heer's *aventica* (*vindobonensis*) is intermediate in form between this species and *œningensis*. Ludwig's *incisa* also includes very similar leaves which have, however, narrower, less incurved, and more rectangularly placed lobes. Whether this species spread from Greece to Japan or from Japan to Greece *via* southern Asia is problematical, but it was probably more plentiful throughout parts of southern Asia and on the hills of the incipient Himalayas than the fossils indicate. The leaf from British Columbia which Dawson referred to *Comptonia cuspidata* Lesq. differs from that species in size and in the shape of the lobes. It is somewhat smaller than Unger's type material of *dryandroides* but is identical with the Japanese leaf referred here. Dawson says (p. 81): "Allied with *œningensis* Heer, *obtusiloba* Brongn., and *dryandroides* Ung. all of which may be varieties of one species." To *œningensis* I fail to see any resemblance except in the tip which is a variable character of little weight. What Dawson means by *obtusiloba* Brongn. I have not been able to make out.

Comptonia cuspidata Lesq.

Comptonia cuspidata Lesq., *Proc. U. S. Nat. Mus.*, vol. 5, p. 445, pl. 6, fig. 10–12, 1883.

Myrica (*Comptonia*) *cuspidata* (Lesq.) Knowlton, *Proc. U. S. Nat. Mus.*, vol. 17, p. 221, 1894; *Ann. Rep. U. S. Geol. Surv.*, vol. 17, pt. 1, p. 885, 1896 (*non* Dawson).

This must have been a particularly beautiful plant with its large, almost falcately lobed leaves. That these acute, upwardly directed

lobes are not anomalies is indicated by the three leaves that Lesquereux figures, which are of widely different sizes, his larger figure indicating a leaf about fifteen centimeters in length and showing perfectly the characteristic venation of this genus.

Lesquereux compares this species with *Comptonia acutiloba* Brongn., to which, however, the resemblance is not especially close, not so close as it is, for instance, to Ludwig's larger figure of *Comptonia incisa* (*gaudinii* Heer). In both of these species, however, the lobes are laterally pointed and not ascending. The European leaf which is the closest to *cuspidata* is Unger's specimen of *dryandroides* from the Oligocene of Styria, in which the resemblance is quite striking although the lobes of the latter are somewhat less ascending.

The occurrence of *Comptonia cuspidata* and *premissa* in Alaska during the early Tertiary would seem to indicate that they represent the invasion of the genus into Asia from the Arctica-North America region which probably shortly preceded or followed this Alaskan occurrence, as they are not so different from the two forms which occur in the Miocene of Japan as to preclude the idea of their standing in ancestral relations to the latter.

Comptonia premissa Lesq.

Comptonia p emissa Lesq., *Proc. U. S. Nat. Mus.*, vol. 5, p. 445, pl. 6, fig. 13, 1883.
Myrica (*Comptonia*) *premissa* (Lesq.) Knowlton, *Ibid.*, vol. 17, p. 222, 1894; *Ann. Rep. U. S. Geol. Surv.*, vol. 17, pt. 1, p. 885, 1896.

This lower Tertiary species from Coal Harbor and Chignik Bay, Alaska, had leaves very similar to the younger leaves of the living species of Comptonia and not especially close to any of its known European contemporaries. Were the remains of Heer's *laharpii* more definite it might possibly be compared with the Alaskan form, while Sternberg's type figure (*Fl. d. Vorwelt*, Pl. 24, Fig. 1) of *Comptonia diforme* shows the closest resemblance to it of any of the forms known to me.

Comptonia gracillima (Heer) Berry

Dryandra gracilis Heer, *Fl. Tert. Helv.*, vol. 3, p. 311 (note), 1859.
Myrica gracillima (Heer) Schimp., *Pal. Végét.*, vol. 2, p. 559, 1872.

?Myrica minima Sap., *Etudes*, vol. 1, p. 199, 1863.
Schimp., *loc. cit.*, p. 562.
?Myrica pusilla Sap., *loc. cit.*
Schimp., *loc. cit.*, p. 561.

Heer's species was from the Oligocene of Spechbach in Alsatia while Saporta's were both from the Oligocene of Saint Zacharie in France. These three species, so called, are all from strata of about the same age, and not widely removed geographically, none are figured by their authors, they are all founded on very small obtusely lobed leaves, and while they may represent one or more valid species of small size, it seems more probable that they are founded upon immature leaves such as are so common on terminal shoots in close proximity to the fruit in the modern species, of one of the dominant Oligocene species, *Comptonia schrankii* for instance.

I have united them provisionally under Heer's name, which has priority, since if left as distinct forms they indicate an abundance and variety of species of Comptonia which is apt to be very misleading when based upon such insufficient evidence.

Comptonia grandifolia Unger

Comptonia grandifolia Unger, *Chlor. Protog.* (inedit.); *Synopsis*, p. 213, 1845; *Gen. et Sp.*, p. 394, 1850; *Foss. Fl. v. Sotzka*, p. 31 (161), pl. 8 (29), fig. 1, 1850; *Foss. Fl. v. Radoboj*, p. 161, 1869.
Brongn., *Tabl.* p. 118, 1849.
Dryandroides grandifolius Ettings., *Proteac. d. Vorwelt*, p. 34 (742), pl. 5, fig. 2, 1851.

This species is founded upon rather poor and indefinite remains of a gigantic leaf with obsolete secondary venation from the lower Miocene (Mayencian) of Radoboj in Croatia. The specimen is 5.5 cm. wide across the more perfect lobes, while the largest leaf of the existing Comptonia which I have been able to find is 3.5 cm. wide, or seven elevenths of the size of the Radoboj leaf. Large-leaved fossil Comptonias of undoubted authenticity are *magnifica* of Watelet which is 3.2 cm. wide, and *matheroniana* of Saporta which is 3.8 cm. in width. *Comptonia grandifolia* is almost identical in size and outline with the leaves of the existing *Banksia*

grandis Willd. as pointed out by Ettingshausen (*loc. cit.*) so that its reference to Comptonia may be regarded as largely problematical.

Comptonia suessionensis Watelet

Comptonia suessionensis Wat., *Pl. Foss. Bass. d. Paris*, p. 122, pl. 33, fig. 2, 1866.
Myrica suessionensis (Wat.) Schimp., *Pal. Végét.*, vol. 2, p. 553, 1872.

A rather large leaf, exceptionally broad considering its narrow lobes, somewhat similar to the leaf of the existing species shown on Pl. 2, Fig. 2. Watelet's figure shows us a curious combination of rounded and acute lobes, and it seems quite probable that his specimen is not correctly depicted. Schimper (*loc. cit.*) says that this species greatly resembles *Myrica dryandræfolia* Brongn. (*Comptonia schrankii*) but I fail to detect any very close resemblance.

With considerable doubt regarding the propriety of retaining this as a valid species, I still see no other disposition to make of it at present.

Comptonia laciniata Unger

Comptonia laciniata Unger, *Gen. et Sp.*, p. 394, 1850; *Foss. Fl. v. Parschlug*, p. 35, 1848; *Foss. Fl. v. Sotzka*, p. 31, pl. 8, fig. 2, 1850; *Iconogr.*, p. 33, pl. 16, fig. 8, 1852 (aments); *Foss. Fl. v. Radoboj*, p. 161, 1869; *Fl. Tert. Asia Mineur in Tschitacheff, Asia Min.*, pt. 4, p. 320, 1869.
Brongn., *Tabl.*, p. 121, 1849.
Dryandroides laciniatus Ettings., *Proteac. d. Voruv.*, p. 33, 1851.
Myrica ungeri Heer, *Fl. Tert. Helv.*, vol. 2, p. 35, pl. 70, fig. 7, 8, 1856.
Ibid., vol. 3, p. 176, pl. 150, fig. 22 (fruit)?, 1859 (*non* fig. 21, which is referable to *vindobonensis*).
Massal., *Pianti. Terz. Vicentino*, pp. 243, 258, 1851.
Schimp., *Pal. Végét.*, vol. 2, p. 556, 1872; *Atlas*, pl. 85, fig. 8, 1874.
Lesq., *Proc. U. S. Nat. Mus.*, vol. 11, p. 27, 1888.
Boulay, "Fl. Foss. Gergov.", *Ann. Sci. Brux.*, 1899, pp. 59, 131.
(*Non* Ludw., *Palæont.*, vol. 8, p. 95, pl. 29, fig. 2, 2a; pl. 30, fig. 2, 3, 1860.)
Myrica græffii Heer, *Fl. Tert. Helv.*, vol. 3, p. 176, pl. 150, fig. 19, 1859 (*non* fig. 20 which is referable to *vindobonensis*).

This is a beautiful species with large leaves some fifteen centimeters in length and upwards of three centimeters in width, irregularly lobed; each lobe with one or more serrations of the margin besides the rather larger, somewhat falcate, usually pointed tip. There is considerable variation in the depth of the sinuses, Unger's type figure from Sotzka showing a leaf with deep sharp sinuses, while the handsome specimen figured by Heer (*loc. cit.*, Pl. 70, Fig. 7) has more shallow and slightly rounded sinuses. The sharpness of the serrations and tips of the lobes tends to be much softened in the basal and apical portions of the leaves, in fact one of the leaves figured by Heer has them distinctly rounded.

As remarked under *Comptonia vindobonensis*, some of the leaves of that species are quite close to this one and are also represented by variations of the modern leaf, an example of which is figured on Pl. 2, Fig. 5. The latter, while shorter and not exactly similar to *laciniata*, has precisely the same character of serrated lobes. Unger observed in the collections from Parschlug, Styria, a staminate inflorescence which he says is indistinguishable from that of the existing Comptonia and which he refers to *laciniata*.

This species appears in some numbers in the late Oligocene of the upper Rhone and Jura regions of central Europe and continues into the Upper Miocene (Tortonian) of Styria. It has been recorded by Lesquereux from Spanish Peak, California, but was not figured and I have been unable to locate the material upon which his determination rests, so that this occurrence may be considered very doubtful for the reason that undoubted Myrica species have leaves which are not very different from *laciniata*. This is especially to be seen in the leaves from Florissant, Col., and Wycliffe, Ky., which Lesquereux named *Myrica copeana*, regarding which I found it impossible to reach a decision until after consulting the type material in the U. S. National Museum.

Comptonia matheroniana (Sap.) Berry

Myrica (*Comptonia*) *matheroniana* Sap., *Etudes*, vol. 2, p. 93, pl. 5, fig. 7, 1865.

Schimp., *Pal. Végét.*, vol. 2, p. 555, 1872; vol. 3, p. 691; *Atlas*, pl. 55, fig. 10, 1874.

Boulay, *Fl. Foss. Gergov.*, p. 73, 1899.
Probst, *Jahresb. vaterl. Naturk. Würtemberg*, p. 190, 1883.
Comptonia magnifica Watelet, *Pl. Foss. Bass. Paris*, p. 123, pl. 33, fig. 3, 1866.
Myrica magnifica (Wat.) Schimp., *loc. cit.*, vol. 2, p. 554, 1872.

Leaves of extremely large size with lobes similar to the normal lobes in the leaves of the existing species. Saporta's leaf is only slightly larger, however, than the modern leaf shown in Pl. 2, Fig. 6.

The Eocene and Oligocene forms are very similar, what little differences are apparent being probably due to the careless drawing of the leaves from the Paris basin. Saporta's figure, however, does show a few serrations on some of the lower lobes which are wanting in its Eocene ancestor, if we may draw such a conclusion from the small amount of material available for study. I was at first inclined to keep these two leaves separate, appearing as they do at such different horizons, but there are a number of other identical species from the two horizons, and others with even a greater range in the Cenozoic, so that it has seemed best to unite them as above indicated. It is, of course, within the range of possibility that they do not constitute a valid species but in each case are simply abnormally large leaves of contemporary and smaller-leaved forms; for instance, Watelet's leaf might be merely a giant leaf of the Belleu species which he named *triangulata* (*gaudinii* Heer). Schimper notes the resemblance of these leaves to such Proteaceous forms as those of *Banksia grandis* and *repens* of Robert Brown, but the resemblance is much closer to the large leaves of the modern Comptonia. Saporta in his revision of the Aix flora records this species from that locality and notes its resemblance to *Myrica aculeata.*

Comptonia microphylla (Heer) Berry

Myrica (*Comptonia*) *parvula* Heer, *Fl. Foss. Arct.*, vol. 7, p. 20, pl. 55, fig. 1–3, 1883.
Newberry, *Fl. Amboy Clays*, p. 63, pl. 19, fig. 6, 1896.
Myrica (*Comptonia*) *parvifolia* Heer, *loc. cit.*, p. 77, pl. 71, fig. 12, 1883.
Rhus microphylla Heer, *loc. cit.*, vol. 3, pt. 2, p. 117, pl. 32, fig. 18, 1874.

It is difficult to understand upon what ground Heer founds his two species *parvula* and *parvifolia* unless it is because they are from different horizons. He compares both to the European *Myrica œningensis* (Braun) Heer, although their resemblance to that species, as a matter of fact, is not very close.

The two are exactly similar except that the form *parvifolia* is somewhat the larger. The Raritan leaf which Newberry refers to *parvula* is more like *parvifolia*, which fact is noted by the latter author, who, I suppose, hesitated about referring a Cretaceous leaf to a species of the late Miocene as these Arctic deposits were thought to be at that time.

I can see no reason for maintaining them as separate species, even though one is Cretaceous and the other Tertiary, a statement not altogether beyond question in view of the fact that labels are sometimes misplaced, and in the case of *parvifolia* the name was based upon a single imperfect specimen which might readily enough become included with other collections from earlier strata, both having been collected by Professor Steenstrup's expedition. In addition to the above, it may be remarked that the exact age of the Greenland Tertiary deposits has never been definitely and satisfactorily settled, and in all probability the Atanekerdluk deposits are not younger than the Oligocene and more probably are upper Eocene.

The first five or six leaves on young plants of the existing *Comptonia peregrina* (Linn.) Coulter usually closely resemble this fossil species both in size and in shape. This is well shown by a comparison of the figures which I have reproduced; in fact the existing leaves were they to occur as fossils would unhesitatingly be referred to *parvula* Heer, some of them being exact duplicates of this fossil leaf. Heer's Fig. 1 which shows a more primitive leaf than his other figures, finds its counterpart in the first leaf of the modern seedling, which is almost equally close to the types of *Comptonia microphylla* and *antiqua*. I have collected a large number of leaves of this form, and find this type with more or less accentuation to be present in all the seedlings which I have examined.

We might consider these fossil leaves to be merely the abbreviated leaves which are so common in seedling plants and hence without phylogenetic meaning, or we might consider that this form of fossil

leaf represented the normal leaves of ancient Comptonia plants. The former view seems to me doubtful, not only because of the perishable nature of seedling leaves in general, but because it is unusual for them to become detached and fossilized. That they are sometimes found as fossils is proven by the leaves from the Swiss Tertiary which Heer calls *Myrica latiloba* (*Fl. Tert. Helv.*, vol. 3, p. 176, pl. 150, figs. 12–15, 1859). Furthermore no other species of Comptonia has been found in the Raritan clays or Patoot schists from which they could have been derived. We are quite justified in concluding that these leaves are the normal leaves of the earliest known Comptonias and that the modern seedling leaves are truly atavistic. From the abundance of the genus Myrica with nine species in the Raritan, we may assume that the Comptonia stock became separated from Myrica some time during the lower Cretaceous, probably toward its close. While the leaf which Heer calls Rhus is probably from a slightly higher horizon than the Raritan leaf, its smaller size and its occurrence near what was probably the original center of radiation of the genus Comptonia, stamp it as the real starting point for any scheme of Comptonia phylogeny and distribution, and also emphasize the close relation, if not actual identity, between these forms of the New World and *Comptonia antiqua* Nilss. of Europe.

There are four species of Myrica in the Atane flora and two in that of Patoot; one of the latter (*præcox*) Heer considers as referable to Comptonia. While I do not agree in this reference, the species in question might be considered as showing the close relation between Myrica and Comptonia at this time, although I am strongly inclined to think that *Myrica præcox* is a Quercus, to which genus all of the early Comptonias show a passing resemblance, particularly the Raritan leaf.

Comptonia œningensis Al. Br.

Comptonia œningensis Al. Br., *Neues Jahrb. f. Miner.*, p. 108, 1845; *Verz. foss. Pfl. v. Œningen*, p. 76, 1851.
Unger, *Gen. et. Sp.*, p. 394, 1850; *Foss. Fl. v. Sotzka*, p. 32 (162), pl. 8 (29), fig. 3, 1850.
Brongn., *Tabl.*, p. 121, 1849.
Massal., *Pianti Terz. Vicent.*, p. 243, 1851.

Dryandra æningensis Ettings., *Proteac. d. Vorw.*, p. 28, 1851.
Myrica æningensis (Al. Br.) Heer, *Fl. Tert. Helv.*, vol. 2, p. 33, pl. 70, fig. 1–4, 1856; *Ibid.*, vol. 3, p. 175, pl. 150, fig. 18, 1859.
Schimp., *Pal. Végét.*, vol. 2, p. 557, 1872; *Atlas*, pl. 85, fig. 9, 1874.
Comptonia meneghinii Unger, *Foss. Fl. v. Sotzka*, p. 32 (162), pl. 8 (29), fig. 10, 1850.
Massal., *loc. cit.*, pp. 47, 243.
Dryandra meneghinii Ettings., *loc. cit.*, p. 28.
Myrica meneghinii (Unger) Schimp., *loc. cit.*, p. 555.

Schimper was the first to notice the resemblance of Unger's *Comptonia meneghinii* to *Comptonia æningensis*, a resemblance so close that I have been constrained to consider the two forms identical, an additional reason for this treatment being the unimportance of the remains of the former. Ettingshausen refers both forms to *Dryandra*, comparing the former with *Dryandra obtusa* and *plumosa* of Robert Brown and the latter with the same author's *Dryandra floribunda* and *cuneata*. It may be noted that their texture is much more membranaceous than obtains in the genus Dryandra. The species may be defined as including medium and rather small leaves of the general proportions of the modern leaf, with triangular, ascending, pointed, obtuse-tipped lobes. Incisions reaching only part way to the midrib. Base cuneate, more produced than in any specimens of the modern leaf that I have seen. The apex is also produced and shows but incipient indications of lobation.

These leaves approach very near to *Comptonia vindobonensis*, particularly to the Swiss leaves of that species, with which they are almost identical.

Comptonia obtusiloba Heer

Myrica (*Comptonia*) *obtusiloba* Heer, *Uebers. Tertiarfl. d. Schw.*, p. 52, 1854; *Fl. Tert. Helv.*, vol. 2, p. 35, pl. 70, fig. 10, 1856.
Saporta, *Etudes*, vol. 2, p. 105, pl. 5, fig. 7, 1865.
Schimp., *Pal. Végét.*, vol. 2, p. 560, 1872.
Ettings., *Blattskel. Dikot.*, p. 3.
Boulay, "Fl. foss. Gergov.," *Ann. Sci. Brux.*, vol. 23, p. 59, 1899.
Myrica laharpii Heer, *Fl. Tert. Helv.*, vol. 2, p. 34, pl. 70, fig. 11, 12 1856.
Schimp., *loc. cit.*, p. 559.

Myrica rotundiloba Sap., *loc. cit.*, vol. 1, p. 200; vol. 2, p. 46, pl. 5, fig. 3, 1865.
Schimp., *loc. cit.*, p. 554.

Includes leaves with poorly developed, rather irregularly rounded lobes, Saporta's specimen from St. Zacharie showing a few remote serrations. Both the form known as *rotundiloba* Sap., and *laharpii* Heer apparently represent anomalous leaves, the former occurring only as a single fragment and the latter consisting of very imperfect material which Heer says is similar to various Proteaceous leaves except for the thin midrib. The type material of *obtusiloba* is considered by Heer to be very similar to the Sotzka leaves of *acutiloba*, but I fail to see such a resemblance. The *laharpii* form is very similar in outline to Watelet's *Comptonia pedunculata* from the French Eocene, and Saporta notes the close similarity between his *rotundiloba* and Heer's *laharpii*.

The various remains which I have included in this species are all somewhat indefinite in form and venation, and without uniformity in lobal characters, so that they shed but little light upon the relations of the plants which bore them, to the other species of Comptonia.

Comptonia partita (Lesq.) Berry

Myrica partita Lesq., *Ann. Rep. U. S. Geol. Surv. Terr. for 1873*, p. 412, 1874; *Tert. Fl.*, p. 134, pl. 17, fig. 14, 1878.

This subcoriaceous fragment, consisting of but two lobes on each side, was collected by Professor Cope from the Eocene of Nevada. Lesquereux compares it with *œningensis* of Braun, and, except for the margin, which was denticulate on the lower border of the lobes, with *incisa* of Ludwig. It is entirely indefinite in character and simply serves to show that there was in the American Eocene, a Comptonia species with leaves of the same general type as the species *gaudinii* Heer, *dryandroides* Unger, and *diforme* Sternb., which are so common in the European Tertiary. The Miocene of British Columbia furnished Dawson with a leaf that he called *Comptonia columbiana* which is almost

identical with *partita* although I prefer to consider it more closely related to *diforme*. The occurrence of the latter in the late Tertiary in connection with the occurrence of *partita* in the early Tertiary renders it almost certain that Comptonia was better represented and with more widely ranging species in the American Tertiary that the fossil remains hitherto found would indicate, and this is just what we would anticipate from the European evidence.

Comptonia pedunculata Watelet

Comptonia pedunculata Watelet, *Pl. Foss. Bass. Paris*, p. 124, pl. 33, fig. 5, 6, 1866.
Myrica pedunculata Schimp., *Pal. Végét.*, vol. 2, p. 555, 1872.
Comptonia rotundata Watelet, *loc. cit.*, fig. 7.
Friedrich, "Beitr. z. Kennt. Tertfl. Sachsen," *Abh. geol. Spk. Preuss. u. Thüring.*, vol. 4, p. 221, pl. 29, figs. 15, 15a, 1883.

All of Watelet's figures in the work cited above have the appearance, both in the venation and outline depicted, of having had the testimony of the specimens largely supplemented by the imagination of the artist. Especially is this true of the leaves which he calls *Comptonia pedunculata* and *Comptonia rotundata*. However, we cannot but consider these two forms when combined, to be entitled to specific rank especially as similar leaves have come to light in the lower Oligocene of Saxony, Watelet's types coming from the Eocene (Sables de Bracheux) of Belleu, France. The species is well named *pedunculata*, as Watelet's Fig. 6 has the longest petiole of any Comptonia leaf that I have ever seen, it being several times the length of the petioles in the existing species. Examples of leaves of the latter that greatly resemble the fossil species in outline, are often found among the larger leaves. While the fossil leaves apparently show rounded lobes with but slight incisions, it is probable that the rather full lobes overlapped as they do in so many leaves of the modern species, and that in reality the lobes were distinct as they were in the latter.

In its rounded margins *pedunculata* approaches *laharpii* Heer (*obtusiloba*) although I think that this is only an apparent similarity. Reasoning from the analogy furnished by the abundant

rounded-lobed leaves of the existing species it would be a reasonable conclusion that *pedunculata* is simply a round-lobed form of some of its normally lobed contemporaries, which one, of course, it is impossible to say, but not necessarily the same species in the Oligocene as in the Eocene.

Comptonia schrankii (Sternb.) Berry

Asplenioptéris schrankii Sternb., *Fl. Vorwelt*, vol. 2, p. 29, pl. 21, fig. 2, 1822; vol. 4, p. 22, 1825.

Comptonia ? dryandræfolia Brongn., *Ann. Sci. Nat.*, ser. 1, vol. 15, p. 49, pl. 3, fig. 7, 1828 (Schimper, *Pal. Végét.*, vol. 2, p. 808, erroneously cites vol. 4); *Prodrome*, pp. 143, 214, 1828; *Tabl.*, p. 118, 1849.
Unger, *Synopsis*, p. 213, 1845; *Gen. et Sp.*, p. 393, 1850.
Squinabol., *Cont. Fl. Foss. Terz. Liguria*, pt. 4, p. 17, 1892.
Massal, *Sopra Pianti Foss. Terr. Terz. Vicentino*, pp. 243, 258, 1851.

Myrica (*Comptonia*) *dryandræfolia* Saporta, *Etudes*, vol. 2, p. 104, pl. 5, fig. 8, 1865 (reproduced in Schimp., *Pal. Végét.*, pl. 85, fig. 19–21).

Dryandra schrankii Ettings., *Proteac. d. Vorw.*, p. 26, pl. 3, fig. 1–8, 1851; *Fl. v. Häring*, p. 55, pl. 19, fig. 1–26, 1853; *Foss. Fl. Monte Promina*, p. 34, pl. 14, fig. 5, 6, 1855.
Web. & Wess., *Palæont.*, vol. 4, p. 147 (37), pl. 25 (6), fig. 12, 1856.

Myrica brongniarti (Ettings.) Lesq., *Ann. Rep. U. S. Geol. & Geog. Surv. Terr., for 1873*, p. 412, 1874; *Tertiary Flora*, p. 135, pl. 17, fig. 15, 1878.

Comptonia breviloba Brongn., in Sedg. & Murch., *Trans. Geol. Soc. Lond.*, ser. 11, vol. 3, p. 373, 1832; *Tabl.*, p. 118, 1849.
Unger, *Synopsis*, pp. 213, 305, 1845; *Gen. et Sp.*, p. 349, 1850; *Foss. Fl. v. Sotzka*, p. 32, pl. 8, fig. 9, 1850.

Comptonites dryandræfolius Göpp. in Bronn, *Ind. Palæont.*, vol. 1, p. 322, 1848; vol. 2, p. 45, 1849.

Leaves of this species were described and figured by Sternberg as early as 1822. He thought that he was dealing with a fern and used the generic name *Asplenioptéris*. With the exception of the somewhat doubtful specimen from the Green River group (Eocene) which Lesquereux refers to *Myrica brongniarti*, the species is confined to Europe, where it is quite common and extends from the Eocene of the Isle of Wight up through the Miocene, becoming especially common and widespread during the Oligocene and Miocene. I have shown on Pl. 2, Fig. 1, a leaf of the existing species which is very close to this species, particularly

to that size and form of leaf figured by Brongniart. Both Ettingshausen and Heer, partially followed by Schimper, consider the leaves referred to the various species in the foregoing synonymy, as identical and they compare them with the leaves of the living *Dryandra formosa* R. Br. They exclude them from Comptonia because of their thick midrib, acute lobes, and coriaceous texture, exactly the characters in numerous instances of the young leaves near the growing tips in the existing Comptonia. I do not think that there can be any doubt regarding the identity of these fossil forms and I fail to see any characters which weigh against their reference to Comptonia unless it be their comparatively greater length. Some of the forms are characteristically those of Comptonia, *e. g.*, some of the leaves from Monte Promina and Häring, which also form a transition series toward *Comptonia diforme;* and these leaves gradually vary to the slender and acutely lobed forms. If comparisons are made with a large enough series of leaves of the existing species, many resemblances will at once become apparent, especially as remarked, to the slender, coriaceous, thick-veined leaves of the tips of shoots. The latter are not usually acutely lobed but often have that appearance in leaves not completely unfolded, or in herbarium specimens in which the lobes have become somewhat involuted in drying, as they usually do. In this condition they are indistinguishable from the fossil specimens. The American leaf of Lesquereux which is included in this species is less incised than the foreign forms and has rounded lobes. It is connected with the more typical leaves by the form described by Web. & Wess. from Rhenish Prussia. Engelhardt in his "Tertiärflora Jesuitengrabens bei Kundratitz in Nordböhmen"[1] figures what he considers catkins of Myrica. His figures look much more like leaves of this species, however, than they do like catkins.

Comptonia vindobonensis (Ettings.) Berry

Dryandra vindobonensis Ettings., *Tert. Fl. v. Wien*, p. 18, pl. 3, fig. 6, 1851.

Dryandroides concinna Heer, *Fl. Tert. Helv.*, vol. 3, p. 188, pl. 153, fig. 8–10, 1859.

[1] *Nova Acta Leop. Carol.*, vol. 48, no. 3, pl. 8, fig. 10, 11, 1885.

Dryandroides bituminosa Sap., *Exam. Anal. Fl. Tert. Provence*, p. 22, 1861.
Dryandra aventica Heer, *loc. cit.*, p. 186, pl. 153, fig. 17.
Dryandra Rolleana Heer, *Ibid.*, (footnote), pl. 153, fig. 18.
Myricophyllum bituminosum Sap., *Etudes*, vol. 1, p. 221, pl. 8, fig. 1, 1863.
Myrica (*Comptonia*) *vindobonensis* Heer, *loc. cit.*, vol. 2, p. 34, pl. 70, fig. 5, 6, 1856.
Myrica vindobonensis (Ettings.) Heer, *loc. cit.*, vol. 3, p. 176, pl. 150, fig. 16, 17, 1859; *Fl. Foss. Arct.*, vol. 2, pt. 2, p. 27, pl. 3, fig. 4, 5, 1869; *Mioc. Baltic Fl.*, p. 32, pl. 7, fig. 4–10, 1869.
Ludwig, *Palæont.*, vol. 8, p. 94, pl. 28, fig. 6, 7, 1860.
Unger, *Foss. Fl. v. Kumi*, p. 22, pl. 4, fig. 20–30, 1867.
Schimp., *Pal. Végét.*, vol. 2, p. 558, 1872; *Atlas*, pl. 85, fig. 1, 2, 1874.
Knowlt., *Proc. U. S. Nat. Mus.*, vol. 17, p. 222, 1894; *Ann. Rep. U. S. Geol. Surv.*, vol. 17, pt. 1, p. 885, 1896.
Engelh., *Tertfl. Jesuitengrab. Kundr. in Nordböhm.*, p. 19, pl. 1, fig. 40, 1885; *Verh. k. k. geol. Reichsanstalt*, no. 5, p. 2, 1902.
Myrica Græffii Heer, *loc. cit.*, pl. 150, fig. 20, (*non* fig. 19 which is referable to *Comptonia laciniata*).
Myrica ungeri Heer, *loc. cit.*, p. 176, pl. 150, fig. 21 (*non* fig. 22), 1859.
Ludwig, *loc. cit.*, p. 95, pl. 29, fig. 2, 2a; pl. 30, fig. 2, 3, 1860.
Myrica denticulata Ettings., *Foss. Fl. v. Koflach*, p. 12, pl. 1, fig. 7, 1857.

This species approaches *Comptonia laciniata* quite closely in Unger's leaves from the Grecian Oligocene, which also closely resemble that style of leaf of the modern species shown on Pl. 2, Fig. 5, a type which is not at all rare on certain of the modern plants of Comptonia.

One of the figured leaves which Heer calls *Myrica græffii* is referable to *vindobonensis* and the other to *laciniata*, which shows how closely these two species are related. In the other direction *vindobonensis* approaches quite near to *æningensis*, such leaves for instance as those of Heer from Switzerland and those of Ettingshausen from Koflach coming very near to the last-mentioned species. As is suggested by its extensive synonymy *Comptonia vindobonensis* as here understood, includes somewhat diverse forms, ranging from the small Planera-like leaves from the Baltic region and the Dryandra-like leaves from Switzerland (*concinna*), through the narrow, more elongated, and but slightly lobed leaves of the French Oligocene (Saporta) and Austrian Miocene (Ettingshausen) to the large-lobed leaves from Hesse which Ludwig referred to this species,

and to those from Switzerland which Heer referred to *rolleana* and *aventica*.

These variations while somewhat wide in their extremes include numerous gradating forms and are not at all inconsistent with their reference to a single species, especially when we consider the duration of this form from the Eocene through the Miocene, during which time it spread all over Europe and possibly to America as well.

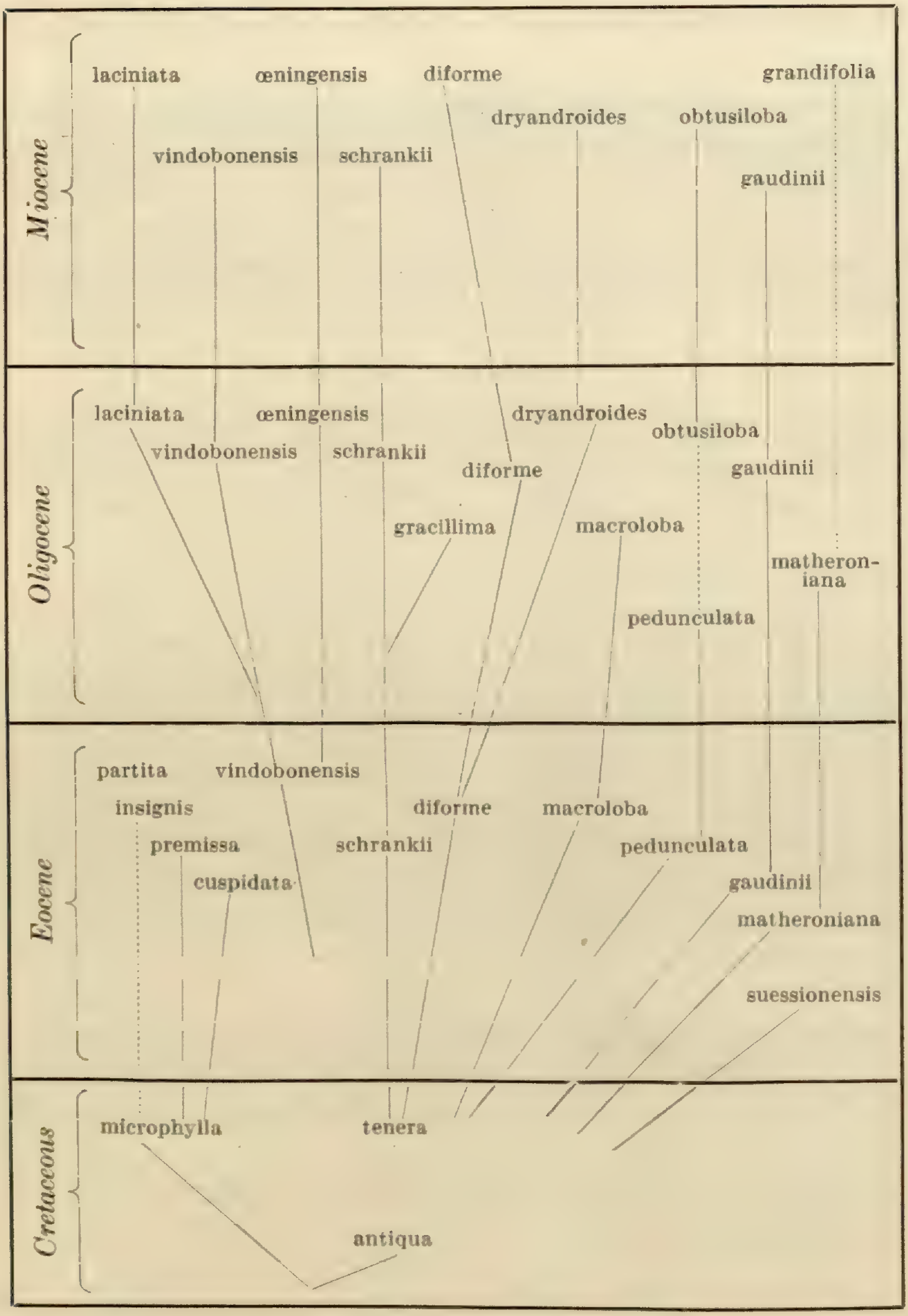
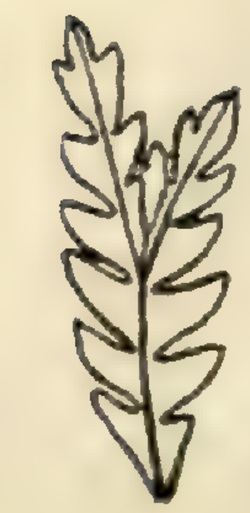


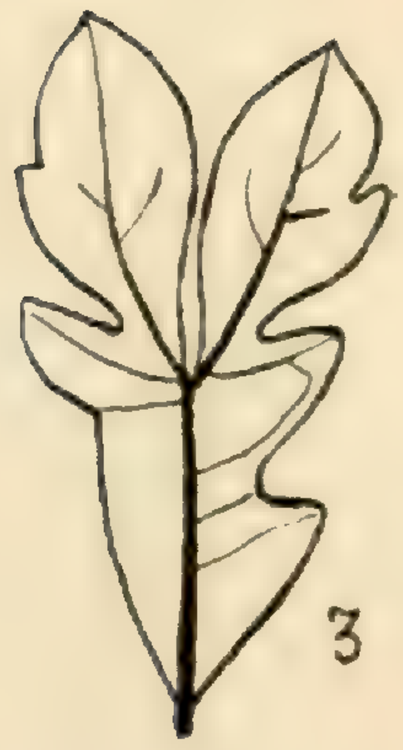
Diagram showing the relationship of the leaves of the fossil species of Comptonia, not necessarily the phylogeny of the plants which bore them.

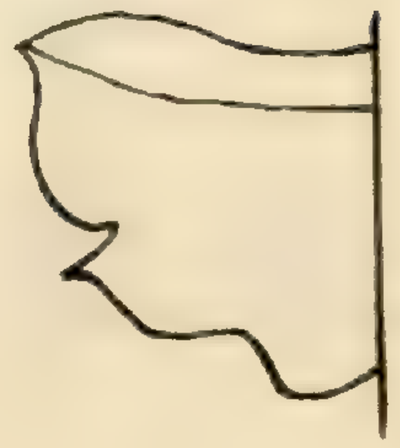
List of Changes in Comptonia Nomenclature

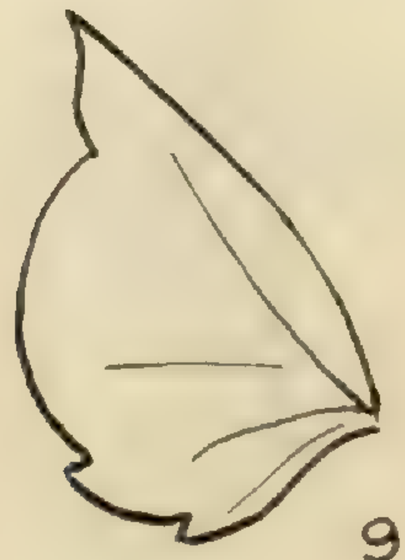
Aspleniopteris difformis Sternb. <*Comptonia diforme* (Sternb.) Berry.
Aspleniopteris schrankii Sternb. <*Comptonia schrankii* (Sternb.) Berry.
Asplenium diforme Sternb. <*Comptonia diforme* (Sternb.) Berry.
Comptonia acutiloba Brongn. <*Comptonia diforme* (Sternb.) Berry.
Comptonia asplenifolia Gaertn.= *Comptonia peregrina* (Linn.) Coulter.
Comptonia breviloba Brongn. <*Comptonia schrankii* (Sternb.) Berry.
Comptonia columbiana Daws. <*Comptonia diforme* (Sternb.) Berry.
Comptonia concisa Wat. < *Comptonia macroloba* (Web. & Wess.) Berry.
Comptonia dryandræfolius Brongn. <*Comptonia schrankii* (Sternb.) Berry.
Comptonia incisa Ludw. <*Comptonia gaudinii* Heer.
Comptonia magnifica Wat. <*Comptonia matheroniana* (Sap.) Berry.
Comptonia meneghinii Ung. <*Comptonia æningensis* Al. Br.
Comptonia rotundata Wat. <*Comptonia pedunculata* Wat.
Comptonia triangulata Wat. <*Comptonia gaudinii* Heer.
Comptonia ulmifolia Ung. <*Planera ungeri* Ettings.
Comptonia vinayi Sap. <*Comptonia diforme* (Sternb.) Berry.
Comptoniphyllum japonicum Nath. <*Comptonia gaudinii* Heer.
Comptoniphyllum naumanni Nath. <*Comptonia dryandroides* Ung.
Comptonites antiquus Nilss.= *Comptonia antiqua* Nilss.
Comptonites dryandræfolius Göpp. <*Comptonia schrankii* (Sternb.) Berry.
Dryandra acutiloba (Brongn.) Ettings. <*Comptonia diforme* (Sternb.) Berry.
Dryandra antiqua Ettings.= *Comptonia antiqua* Nilss.
Dryandra aventica Heer <*Comptonia vindobonensis* (Ettings.) Berry.
Dryandra brongniarti Ettings. <*Comptonia schrankii* (Sternb.) Berry.
Dryandra comptoniæfolia Ettings. <*Comptonia diforme* (Sternb.) Berry.
Dryandra gracilis Heer <*Comptonia gracillima* (Heer) Berry.
Dryandra macroloba Web. & Wess.= *Comptonia macroloba* (W. & W.) Berry.
Dryandra meneghinii Ettings. <*Comptonia æningensis* Al. Br.
Dryandra æningensis Ettings.= *Comptonia æningensis* Al. Br.
Dryandra rolleana Heer <*Comptonia vindobonensis* (Ettings.) Berry.
Dryandra saxonica Friedrich <*Comptonia diforme* (Sternb.) Berry.
Dryandra schrankii Heer <*Comptonia schrankii* (Sternb.) Berry.
Dryandra ungeri Ettings.= *Comptonia dryandroides* Ung.
Dryandra vindobonensis Ettings. <*Comptonia vindobonensis* (Ettings.) Berry.
Dryandroides bituminosa Sap. <*Comptonia vindobonensis* (Ettings.) Berry.
Dryandroides concinna Heer <*Comptonia vindobonensis* (Ettings.) Berry.
Dryandroides grandifolius Ettings.= *Comptonia grandifolia* Ung.
Dryandroides laciniatus Ettings.= *Comptonia laciniata* Ung.
Liquidambar asplenifolia Linn.= *Comptonia peregrina* (Linn.) Coulter.
Liquidambar peregrina Linn.= *Comptonia peregrina* (Linn.) Coulter.
Myrica (*C.*) *acutiloba* Brongn. <*Comptonia diforme* (Sternb.) Berry.

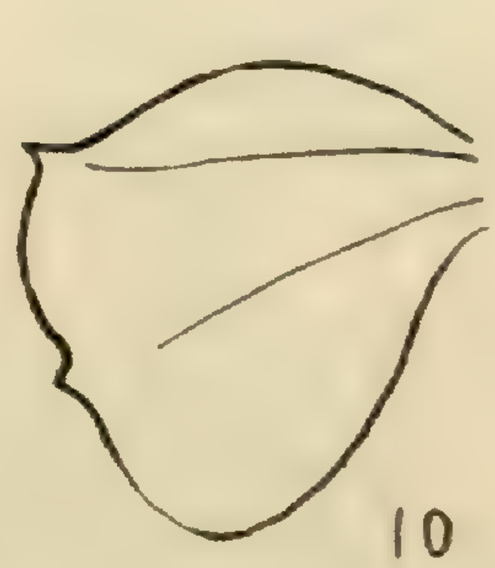
Myrica alkalina Lesq. <*Comptonia insignis* (Lesq.) Berry.
Myrica asplenifolia Linn. = *Comptonia peregrina* (Linn.) Coulter.
Myrica brongniarti (Ettings.) Lesq. <*Comptonia schrankii* (Sternb.) Berry.
Myrica concinna (Heer) Schimp. <*Comptonia vindobonensis* (Ettings.) Berry.
Myrica concisa (Wat.) Schimp. <*Comptonia macroloba* (W. & W.) Berry.
Myrica credneri Engelh. <*Comptonia gaudinii* Heer.
Myrica (*C.*) *cuspidata* (Lesq.) Daws. (*non* Lesq. or Knowlton) <*Comptonia dryandroides* Ung.
Myrica denticulata Ettings. <*Comptonia vindobonensis* (Ettings.) Berry.
Myrica (*C.*) *dryandræfolia* Sap. <*Comptonia schrankii* (Sternb.) Berry.
Myrica (*C.*) *gaudinii* Heer = *Comptonia gaudinii* Heer.
Myrica gracillima (Heer) Schimp. <*Comptonia gracillima* (Heer) Berry.
Myrica grandifolia (Ung.) Schimp. = *Comptonia grandifolia* Ung.
Myrica græffii Heer in part <*Comptonia vindobonensis* (Ettings.) Berry.
in part <*Comptonia laciniata* Ung.
Myrica incisa (Ludw.) Schimp. <*Comptonia gaudinii* Heer.
Myrica insignis Lesq. = *Comptonia insignis* (Lesq.) Berry.
Myrica laharpii Heer <*Comptonia obtusiloba* Heer.
Myrica latiloba Heer = juvenile Comptonia leaves.
Myrica macroloba Web. & Wess. = *Comptonia macroloba* (W. & W.) Berry.
Myrica magnifica (Wat.) Schimp. <*Comptonia matheroniana* (Sap.) Berry.
Myrica (*C.*) *matheroniana* Sap. = *Comptonia matheroniana* (Sap.) Berry.
Myrica meneghinii Ung. <*Comptonia œningensis* Al. Br.
Myrica minima Sap. <*Comptonia gracillima* (Heer) Berry.
Myrica (*C.*) *obtusiloba* Heer = *Comptonia obtusiloba* Heer.
Myrica œningensis (Al. Br.) Heer <*Comptonia œningensis* Al. Br.
Myrica partita Lesq. = *Comptonia partita* (Lesq.) Berry.
Myrica (*C.*) *parvifolia* Heer <*Comptonia microphylla* (Heer) Berry.
Myrica (*C.*) *parvula* Heer <*Comptonia microphylla* (Heer) Berry.
Myrica pedunculata Schimp. = *Comptonia pedunculata* Wat.
Myrica (*C.*) *premissa* (Lesq.) Knowlton = *Comptonia premissa* Lesq.
Myrica pusilla Sap. <*Comptonia gracillima* (Heer) Berry.
Myrica rotundiloba Sap. <*Comptonia obtusiloba* Heer.
Myrica suessionensis (Wat.) Schimp. = *Comptonia suessionensis* Wat.
Myrica (*C.*) *tschernowitziana* Engelh. <*Comptonia gaudinii* Heer.
Myrica ungeri Heer in part <*Comptonia vindobonensis* (Ettings.) Berry.
in part <*Comptonia laciniata* Ung.
Myrica (*C.*) *vindobonensis* Heer <*Comptonia vindobonensis* (Ettings.) Berry.
Myricophyllum bituminosum Sap. <*Comptonia vindobonensis* (Ettings.) Berry.
Phyllites antique Nilss. = *Comptonia antiqua* Nilss.
Pterophyllum difformis Göpp. <*Comptonia schrankii* (Sternb.) Berry.
Rhus microphylla Heer <*Comptonia microphylla* (Heer) Berry.
Zamites difformis Presl. <*Comptonia schrankii* (Sternb.) Berry.











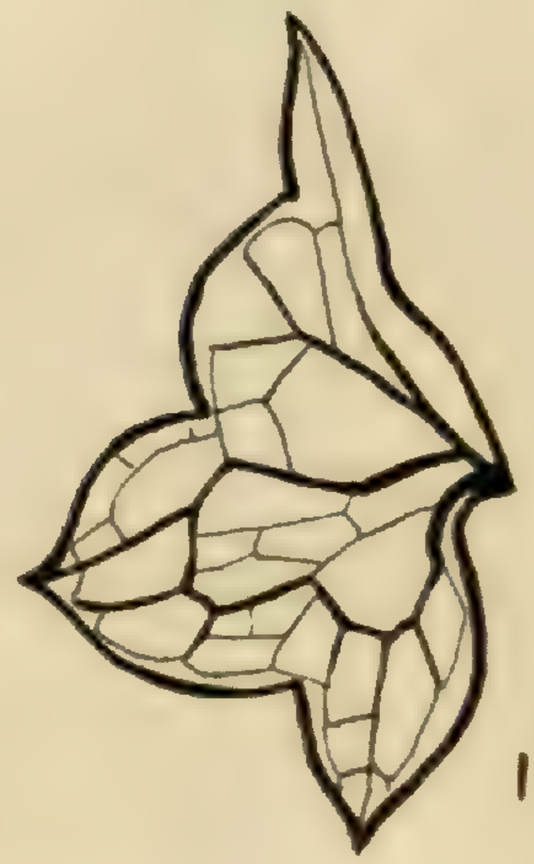


PLATE 1

(Figures somewhat enlarged)

FIGS. 1–3.— Compound leaves of *Comptonia peregrina* (Linn.) Coulter.
FIGS. 4–7.— Basal leaf-lobes of *Comptonia peregrina* (Linn.) Coulter.
FIGS. 8–12.— Stipules of *Comptonia peregrina* (Linn.) Coulter.

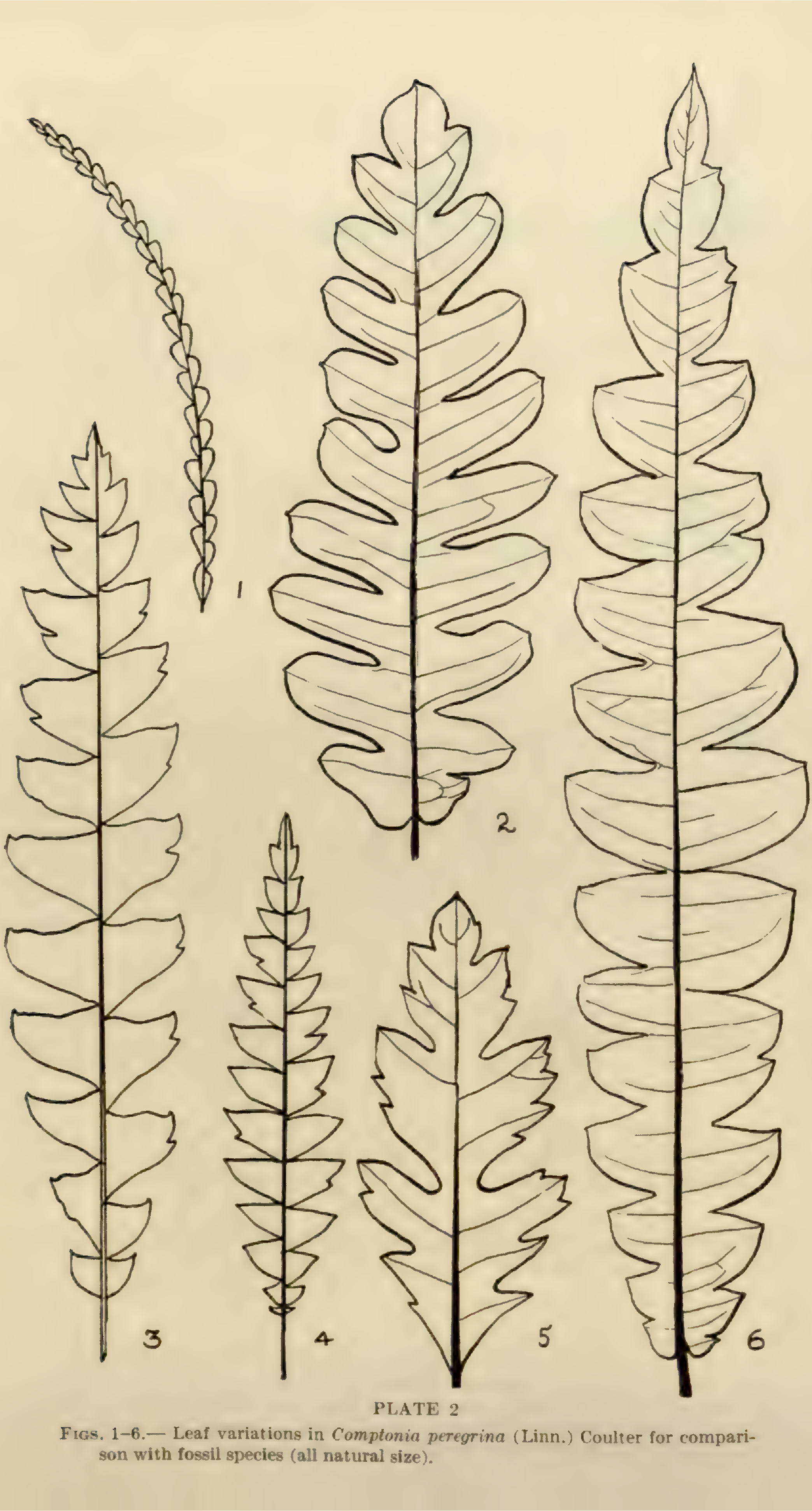


PLATE 2

FIGS. 1–6.— Leaf variations in *Comptonia peregrina* (Linn.) Coulter for comparison with fossil species (all natural size).

PLATE 3

Seedling and leaf variations among juvenile leaves of *Comptonia peregrina* (Linn.) Coulter (all natural size).

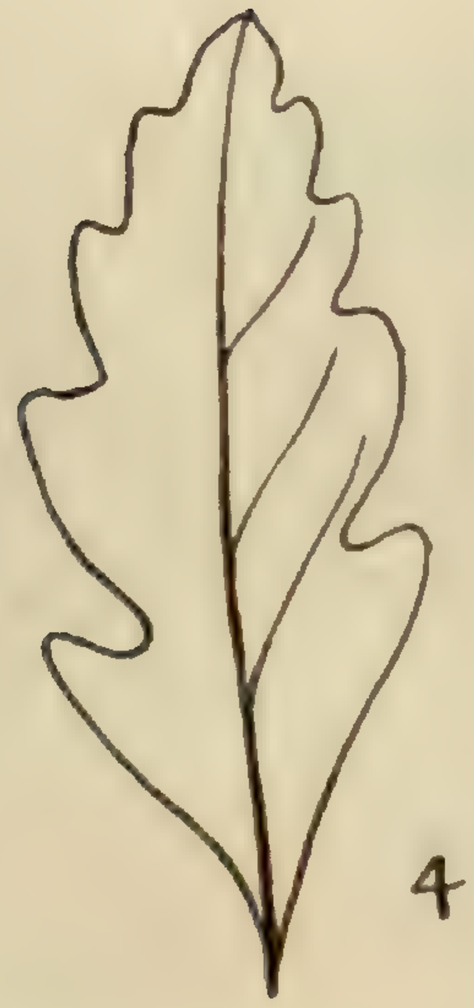


PLATE 4

FIG. 1.— *Comptonia parvula* Heer. After Heer, 1883, Pl. 55, Fig. 1–3.
FIG. 2.— *Comptonia antiqua* Nilss. After Hisinger, 1837, Pl. 34, Fig. 7.
FIG. 3.— *Comptonia parvifolia* Heer. After Heer, 1883, Pl. 71, Fig. 1, 2.
FIG. 4.— *Comptonia parvula* Heer. After Newberry, 1896, Pl. 19, Fig. 6.

NOTES AND LITERATURE

PALEONTOLOGY

Jordan's Guide to the Study of Fishes.[1]— Without question this is one of the most useful and reliable, as it is also the most comprehensive of general works consecrated to the class of fishes. Every subject that is properly included within the domain of ichthyology, whether from a purely scientific, historical, economical, or even Waltonian standpoint,— in fact, all that pertains to fishes living and fossil, — is awarded its place in this repository, and is treated in a manner only possible for the expert of life-long experience. But for the exceptional qualifications of the author, a work of such magnitude and intricacy of details could scarcely have resulted successfully without the coöperation of numerous specialists; the mere labor of bringing together the results of painstaking research during the last few years implies a capacity often regarded as an attribute of genius. Surely the author is to be congratulated upon having accomplished his task so well, and students of ichthyology in general upon having at their command a wealth of carefully analyzed and orderly arranged facts.

Although addressed primarily to students of the modern fauna, this large compendium in two volumes takes ample account of fossil forms. Several of the earlier groups are treated in separate chapters at considerable length, and others are referred to constantly throughout the work. In respect to primitive Devonian fishes, or fish-like vertebrates, the latest contributions of Traquair, Dean, Patten, Regan, and others are passed in review, with mention of newly discovered structural features, and discussion of latest proposed changes in classification. The chapter on Arthrodires is modeled largely after Dean's recent treatment of the group, hence their exclusion from Dipnoans, a step that we are compelled to regard as retrogressive in view of all the evidence now accumulated in favor of their union. It is also to be regretted that new cuts have not been introduced to replace several antiquated and misleading figures of Ostracophores, and even "Ganoids." Scientific text-books often remind us that the law of the

[1]Jordan, D. S. *A Guide to the Study of Fishes.* New York, Henry Holt and Co., 1905. 2 vols., 8vo.

survival of the fittest is apparently reversed in the case of poor illustrations. Figures of recent forms, however, in the work under discussion, are uniformly excellent. Those of the fossil forms that have been washed over may appear more artistic, but certainly have not lost their obscurity. The profusion of illustrations is gratifying as it is remarkable; yet one would willingly spare some of them for greater accuracy of detail in the rest.

No other general treatise on fishes, not even the most recent, can compare with this as regards the fullness with which fossil representatives are discussed in connection with the recent. This is as it should be, and sets a praiseworthy example for other zoölogical writers to emulate. When we have said that the treatment throughout betrays the master hand, the character of the work and its authoritativeness have been sufficiently indicated.

C. R. E.

Lankester's Extinct Animals.[1]— Under this title is collected in book form, of convenient size and well illustrated, the series of paleontological lectures delivered by the Director of the natural history departments of the British Museum during the preceding winter. Since the days of Buckland, Mantell, and Hugh Miller, the British reading public has not lacked popular works for keeping in touch with the progress of paleontological discovery, and for picturing vividly before the imagination the life of bygone ages. Of late years American readers have been even more liberally provided for, through the medium of several first-class popular works, good, bad, and indifferent magazine articles, and the too often absurd exploitations of the Sunday press. Thus there has been no dearth of opportunity for becoming acquainted, in a literary way at least, with creatures of other days.

The new work displays a more rational treatment of the subject than many of its predecessors, there is a more judicious selection and arrangement of facts, and there is constant appeal to the reader to take the book in hand as one would his Baedekker or art museum catalogue, in order to compare the things actually placed on exhibition with what is said about them. This implies, of course, that the majority of readers have access to large public collections; but for those who have not this privilege, more than two hundred illustrations, mostly from

[1]Lankester, E. R. *Extinct Animals.* New York, Henry Holt and Co., 1905. 8vo, 331 pp., 218 figs.

photographs, are provided to supply the deficiency. One of the purposes of these lectures, therefore, is to serve as a sort of museum guide; but this is by no means all. Interwoven with the descriptions of fossil forms is a great deal of explanatory matter which enables the lay reader to gather, as he goes along, trustworthy information in regard to geological phenomena, evolutionary history, the relations between fossil and modern faunas, former conditions of life, and general trend of animal development.

The chapters on mammals and reptiles occupy the greater part of the book, and attention is concentrated upon a limited number of striking examples, illustrative of particular points, so that the confused image resulting from discursive treatment is avoided. The value of the work lies largely in its suggestiveness. A few facts, clearly and sufficiently set forth, intensify the interest and stimulate the quest of knowledge much more than a bewildering array in which there is no visible bond of unity. Professor Lankester reveals to us the beauty of the paleontological landscape by taking us leisurely over some of its hills and dales, and leaves to us our own sense of perspective to fill in the details. There are one or two features, however, that one could wish the author had dwelt upon a little more fully. Many years ago he contributed an admirable monograph on the fishes of the Old Red Sandstone, still a standard authority. We would have liked him to tarry longer in referring to these forms anew. It is to be regretted, also, that the splendid restoration of Diplodocus presented to the British Museum during the year by Mr. Carnegie does not figure in this work, and that the actual skeleton of Triceratops is not shown alongside of Mr. Knight's model. The long supra-occipital crest of Pteranodon, a most striking feature, is unfortunately omitted from the figures that are given of this genus. These, however, are comparatively trifling defects, and are more than offset by the general excellence of illustrations, and conspicuous merit of the descriptive matter.

C. R. E.

Notes. — *Dollo on Iguanodon.* Professor Dollo's researches on Belgian fossil reptiles are well known, in particular those dealing with the famous Dinosaurs of Bernissart. Some further considerations are now offered (Dollo, L., "Les allures des Iguanodons," *Bull. Scient.*, vol. 40, 1905; "Les Dinosauriens adaptés à la vie quadrupède secondaire," *Bull. Soc. Belge Géol.*, vol. 19, pp. 441–448, 1905) concerning the gait of these animals, and such skeletal modifications

as are affected by, or are coördinated with the manner of progression. In the first of these papers an attempt is made to classify different series of footprints according as they were made by the animal in a resting posture, walking, or running; in the second, arguments are advanced to show that certain Dinosaurs are primarily quadrupedal in gait, others secondarily so, as the result of change in function amongst forms which resembled Iguanodon in being primarily bipedal. The arguments are based upon persistence of adaptive characters, and illustrations are drawn from various sources. Dollo's interpretation of tracks suggests the importance of tracing as extended series of footprints made by a single animal as we can find record of in the Newark beds of the Connecticut Valley.

C. R. E.

GEOLOGY

Ries's Economic Geology of the United States[1] is one of the latest text-books on this phase of geology. It is a volume of 435 pages with numerous illustrations, published by the Macmillan Company, in 1905. A novel feature of the volume is the treatment of the non-metallic minerals before the metallic. If the reason for this change — namely, that the most important should be considered first — is justified, it seems strange that the pages devoted to soils should be the very last in the non-metallic portion.

The space allotted to the various subjects is often disproportionate; thus soils are dismissed in four pages, and all the building stones of igneous origin, with the exception of the granites, are treated in fourteen lines.

The plates are very good, but the method of display is not satisfactory, as the pictures are not appropriately placed with respect to the text that refers to them. It is also unfortunate that sometimes two pictures of entirely unrelated features should be placed on the same plate. An example of this is Plate 25; 1, View of Bauxite Bank, etc., 2, Furnace for Roasting Mercury Ores, etc. The proofreading has been well done, the omission of "n" in brownstone on page 69 being practically the only error noted.

[1] Ries, H. *Economic Geology of the United States.* New York, The Macmillan Co., 1905. 8vo, xxi + 435 pp., 25 pls., 97 text figs. $2.60.

Several omissions and slight errors of statement, some of which seem worthy of note are as follows. On page 39, it is stated that until 1883 petroleum was used chiefly for medicinal purposes. This seems rather an understatement of its uses, for, according to the Census figures quoted by the author on page 62, over $26,000,000 worth of petroleum was produced in 1880. On page 111, puzzuolano is described as though it was only an artificially prepared cement, whereas the original material derived from Puzzuoli was natural volcanic ash. The natural cements prepared from volcanic ash receive no notice in the classification used by Ries.

The list of the different clays is quite complete, but the absence of "slip-clay" is noted. This is such an interesting and important group of clays and its value is so largely determined by chemical composition that it deserves some treatment. Another slight error occurs on page 191, were it is stated that the main value of monazite is for "the manufacture of mantles for incandescent lights"— the word incandescent is inapplicable.

One point on which students differ with Professor Ries is the use of the term "thermal" spring. He states that a thermal spring is one whose temperature is 70° Fahrenheit or over (page 204). The old definition, that a thermal spring is one whose temperature is 2° F. above the mean annual temperature of the place of exit, seems in many ways more desirable, for a spring in the tropics with a temperature not higher than 70° F. ought not to be considered a thermal spring, while a spring of 40° or 50° F. in high latitudes should be so considered.

A valuable working bibliography is appended to each chapter, and contains references to many of the latest publications.

P. S. S.

Notes.— The *Geological Magazine* for November and December (decade 5, vol. 2, nos. 11 and 12) contains three articles of general geologic interest. The first, in the November number, is by Professor Jamieson on "Some Changes of Level in the Glacial Period," the region under discussion being mainly Scotland and portions of Scandinavia. The second article, in the December number, on "The Geological History of Victoria Falls," is by G. W. Lamplugh. These falls are particularly interesting on account of the peculiar zigzag pattern of the canyon below the falls. In the December number is also the final paper of Sir H. H. Howorth's article on "The Recent Geological History of the Baltic."

Water Supply and Irrigation Paper 119, by J. C. Hoyt and B. D. Wood, is an "Index to the Hydrographic Progress Reports of the United States Geological Survey from 1888–1903." This is a valuable paper, as it brings together in one volume a bibliography of the papers published by the Survey, which have heretofore not been satisfactorily listed in the bibliographies.

Bulletin 7, Fourth Series, Geological Survey of Ohio, by Charles S. Prosser, published in Columbus, November 1905, and entitled "Revised Nomenclature of the Ohio Geological Formations," is an important contribution to stratigraphy. It successfully presents the results of much detailed study, and places the previously rather loosely defined horizons in their proper positions. It shows not only their relation to each other, but, in a broad way, correlates the formations with those outside the State. *Bulletin 7*, however, is only a preliminary report, so that the final report is awaited with interest.

Two new maps of portions of Alaska are included in the report of L. M. Prindle on "The Gold Placers of Fortymile, Birch Creek and Fairbanks Regions, Alaska"— *Bulletin 251, United States Geological Survey*. The report is based mainly on reconnaissance work, but certain facts seem to have been quite thoroughly worked out. One fact of most general interest is the determination that a large part of the placer gold has been derived from the quartz veins in a series of metamorphic sediments.

The Journada del Meurto of New Mexico is a bolson plain that has long been regarded as one of the most desert regions in the State. Recent studies by Keyes, published in *Water Supply and Irrigation Paper 123*, show that the district affords promise as an artesian basin. The shallow ground-water conditions are not very good, but the porous Cretaceous sandstone which is folded into a syncline and has the impervious Permian red beds at its base, affords good water at a depth of not over 2000 feet, even in the center of the basin. The water is practically fresh, the slight saline scale deposited by evaporation being common salt, so that it is adapted to all domestic purposes.

Bulletin 266 of the United States Geological Survey contains the "Palæontology of the Malone Jurassic Formation of Texas," by Francis Whittemore Cragin, with "Stratigraphic Notes on Malone Mountain and the Surrounding Region near Sierra Blanca, Texas," by T. W. Stanton. The report contains 28 plates of fossils, and one topographic map of the district.

E. C. Eckel has prepared a report on "The Cement Materials and Industry of the United States," which forms *Bulletin 243 of the United States Geological Survey*. The report consists of two distinct portions: first, the technical processes involved in cement manufacture, and second, the distribution of cement materials. The cement materials are divided into the Portland cements, the natural cements, and the Puzzolan cements. The distribution of each of these different cements is treated according to States. The arrangement by States is alphabetical, and consequently necessitates repetition, which would have been avoided if a geological arrangement had been selected. The 15 map plates are of considerable importance, as they present much new and accurate information.

An extremely interesting portion of *Water Supply and Irrigation Paper 105*, by T. U. Taylor, on the "Water Powers of Texas" describes the Austin dam and its destruction, in April, 1900. The failure of the dam seems to be attributable to lack of geologic investigation before construction. This is shown by the fact that the minimum flow of the Colorado was considerably less than supposed, and also that an old watercourse filled with sand, etc., was allowed to remain as a portion of the floor for the foundation of the dam. The photographs reproduced in the text make it evident that the destruction of the dam was not due to weaknesses in the dam itself because not only the dam but also part of the foundation were carried down stream.

"The Water Resources of the Philadelphia District," by Florence Bascom, is published as *Water Supply and Irrigation Paper 106 of the United States Geological Survey*. It contains data concerning the precipitation and run-off for many of the streams. Some of the observations extend over a period of more than thirty years, so that the averages may be considered as characteristic of the district. From these records it appears that in the district as a whole evaporation is in excess of run-off.

A series of five papers regarding the læss of the Mississippi Valley and of Iowa in particular, by Professor Shimek, has recently been received. These papers may be found in the *Bulletin of the Laboratories of Natural History of the State University of Iowa*, (vol. 5, no. 4, pp. 298–381, 1904). These articles support, in a forceful manner, the theory of the æolian origin of læss. Professor Shimek treats particularly the læss of Natchez, the Lansing deposit of so called

læss, in which the Lansing skeleton was found, determining that this deposit is really not læss, and arraigns two or three recent supporters of the aqueo-fluviatile origin of the læss.

The rapid development of underground workings at Cripple Creek and the consequent increase in detailed information has made it desirable to resurvey the field. The results — embodied in *Bulletin 245 of the United States Geological Survey*, "Report of Progress in the Geological Resurvey of the Cripple Creek District, Colorado," by W. Lindgren and F. L. Ransome — furnish an apt illustration of the present efficiency of the Survey. While there are modifications of many of the details previously published concerning the geology of this very complex region, the main facts previously outlined are substantiated. An interesting note in this report states that the depth to which the oxydation of the ore bodies has penetrated is oftentimes a thousand feet.

"A Gazeteer of Indian Territory," by Henry Gannett, forms *Bulletin 248 of the United States Geological Survey*, published in Washington, 1905. In addition to 59 pages devoted to place names, there are 6 pages giving a brief description of the larger topographic features; population, and products.

Two papers concerning certain deposits of economic significance in Illinois, prepared by H. F. Bain, have recently been published by the United States Geological Survey. The first of these is entitled the "Zinc and Lead Deposits of Northwestern Illinois," *Bulletin 246*, and the second is "The Fluospar Deposits of Southern Illinois," *Bulletin 255*. In the former paper, Bain regards the disseminated lead and zinc minerals as having been deposited apparently from sea water and contemporaneously with the sediments in which they occur. In this report, Bain dismisses the other theories of origin in a very peremptory manner, and the reader wonders whether they have been carefully considered.

The volume of "Contributions to Devonian Palæontology for 1903," by H. S. Williams and E. M. Kindle, consists of two distinct parts. The first deals with the Devonian and Mississippian faunas of Virginia, West Virginia, and Kentucky, while the second part treats of the Devonian of central and northern Pennsylvania. The portion of the paper dealing with the Upper Devonian faunas of the middle Appalachians, with a chart showing range of species, is of most general interest. This report is published as *Bulletin 224 of the United States Geological Survey*, and contains 144 pages, 4 plates, and 3 figures.

An interesting preliminary paper by G. O. Smith and F. C. Calkins, entitled "A Geological Reconnaissance across the Cascade Range near the 49th Parallel," is published by the United States Geological Survey as *Bulletin 235*. The paper deals with the geology and petrography of the region traversed. The effect of the prevailing winds, etc., is strikingly shown by the difference in amount of vegetation on the east and west sides of the range, and also on the position and number of glacial *cirques*. A striking illustration of a glaciated valley is shown in Figure B, Plate 3.

Bulletin 245 of the United States Geological Survey, prepared by S. S. Gannett, gives the "Results of Primary Triangulation and Primary Traverse for the Fiscal Year, 1903–1904."

Fuller, Lines, and Veatch have prepared *Bulletin 264 of the United States Geological Survey*, which presents an epitome of the method of work, and an outline of the plan of organization of the Division of Hydrology. The importance of preserving records of the various strata passed through in well-drilling is strongly emphasized. It is proposed to collect not only the written description of the kinds of rock cut, but also to retain a sufficient amount of the original sample to afford a basis for subsequent study and comparison by members of the Survey.

"The Comparison of a Wet and Crucible Method for the Assay of Gold Telluride Ores, with Notes on the Errors Occurring in the Operations of Fire Assay and Parting," by W. F. Hillebrand and E. T. Allen, forms *Bulletin 253 of the United States Geological Survey* publications. The paper deals largely with the chemical methods employed, and concludes that the crucible method is fully as accurate as the wet method.

The cleavage of rocks is treated in *Bulletin 239 of the United States Geological Survey*, a volume of 216 pages, 27 plates, and 40 text figures, by C. K. Leith. The author proposes to divide cleavage into two great groups, original and secondary. Under original cleavage, he includes the parting between bedding planes of sedimentary rocks, flow structure in lavas, concentric jointing in deep-seated igneous rocks, etc. The secondary cleavage structures are divided into two groups, flow cleavage and fracture cleavage. The paper presents a careful investigation, but it may be questioned whether it is desirable to group so many unrelated features under one term.

Bulletin 237 of the United States Geological Survey is a paper by L. V. Pirsson on the "Petrography and Geology of the Igneous Rocks of the Highwood Mts., Montana." The report treats mainly the petrography of this volcanic center, with a brief review of the geology of the district. The portion of general interest is the bearing of this region upon the theories of the consanguinity of lavas.

P. S. S.

CORRESPONDENCE

The Danish Arctic Station

Editor of the American Naturalist

Sir:— In the summer of the present year a permanent station for the study of Arctic science will be established on the south coast of Disco Island in Danish West Greenland. The cost of the foundation is defrayed by a gift from Mr. A. Holck, Counsellor of Justice, of Copenhagen, and the Danish Government has promised an annual grant of kroner 10,000 ($2,500) toward its maintenance.

A laboratory, equipped with appliances and instruments, especially for biological researches, will be attached to the Station, and work places will be furnished for visiting naturalists, foreign as well as Danish. The visitors will have the free use of the instruments, traveling outfit, and library of the Station; lodging will be free and a small fee only will be charged for board. Cheap fare to and from the Station, *via* Copenhagen will be provided. The first visitors can be received in 1907, and notices, inviting application, will be issued in due course.

A library of Arctic literature is to be founded at the Station and to be made as complete as possible, but in view of the limited resources of the Station and the vastness of the Arctic literature, only a small proportion of it can be purchased. As the designed leader of the Station, I venture to ask you therefore, to be good enough to come to its assistance by giving to its library such works on Arctic (and Antarctic) Nature, and, especially on Arctic biology as you may have published or are going to publish in the future. The publications of the Station will, of course, be sent to you in return, and the Station and its leader will be glad to render you any service in their power.

In view of the arrangements to be made for the purchase of books, I would be very grateful to you, if you would inform me at the earliest possible date, whether the present appeal from the Danish Arctic Station will have the favor of your kind consideration.

I am,

Your most obedient servant

MORTEN P. PORSILD

BOTANICAL GARDEN
UNIVERSITY OF COPENHAGEN
DENMARK

(No. 474 was issued June 9, 1906)

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THE AMERICAN NATURALIST

A MONTHLY JOURNAL
DEVOTED TO THE NATURAL SCIENCES
IN THEIR WIDEST SENSE

CONTENTS

		Page
I.	Volant Adaptation in Vertebrates . . . . PROFESSOR R. S. LULL	537
II.	External Morphology of the Dugong PROFESSOR H. DEXLER AND L. FREUND	567
III.	Reproduction of *Metridium marginatum* by Fragmental Fission M. L. HAMMATT	583
IV.	Notes and Literature: *Zoölogy*, Plankton of Northern Seas, *Notes on Pennsylvania Fishes* (H. W. Fowler), *Note on Muhlenberg's Turtle* (H. W. Fowler); *Anthropology*, The Bontoc Igorot, Notes; *Botany*, Plants and Light, Campbell's Mosses and Ferns, Howe's Common and Conspicuous Lichens of New England, Czapek's Biochemistry of Plants, Lacouture's Liverworts of France	603

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AMERICAN NATURALIST

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VOLANT ADAPTATION IN VERTEBRATES

RICHARD S. LULL

OF THE several environments to which vertebrates have become adapted, the two which most profoundly modify their inhabitants are the water and the air. This is in part due to the fact that a homogeneous environment pressing upon all sides of the organism with almost the same intensity has moulded the form into a symmetrical contour which offers but little resistance in passing through the medium. In addition, special modifications of the limbs must occur, supplemented in air-inhabiting forms by cutaneous expansions or appendages for support or propulsion, without which very existence in the medium is out of the question.

Aquatic life modifies its denizens the more profoundly, because it becomes permanently sustaining, while even the best of fliers must ultimately return to the trees, the earth, or the sea. The aërial forms therefore always retain functional structures to enable them to move in the environment from whence their ancestors came. Of the more perfectly adapted aquatic types this is not true.

Creatures, other than the aquatic forms, can exist in the terrestrial realm without special adaptation; many forms which can climb fairly well may hardly be said to exhibit scansorial modification and indeed, while prolonged life in the water profoundly alters the contours of the animal, many vertebrates are fair swimmers whose proper environment is elsewhere. To venture into the aërial realm without an especial equipment for flight is to

court destruction like Darius Green, though many animals which cannot even soar, are wonderful leapers.

With the exception of the Amphibia, every class of vertebrates has developed true flight, while the power of soaring from a higher to a lower level has been acquired again and again.

Altogether no fewer than seventeen separate evolutions for aërial life have occurred among vertebrates, true flight five and probably seven[1] times, and soaring at least ten times. The forms which soar are singularly uniform in the plan of the sustaining mechanism and one would be justified in considering many of the volant mammals as the result of a single evolution were it not for the fact that in many cases the nearest relatives, which might prove annectant, are flightless forms. In true fliers, however, there is in each instance so distinct a plan of structure that there is not the slightest doubt that each has arisen through a separate evolution.

It is necessary to draw a sharp line of demarcation between the soarers and those having true flight, and the latter are again divided according to the mode of progression. These are, to use Marey's terms, the sailers, forms of great wing expanse like the vultures which rise slowly, but once in the air sustain themselves on almost motionless pinions; and the rowers or wing-flappers, such as have limited alar expanse and must make good this lack by a rapid vibration of the wings. This type culminates in the hummingbirds, though including many large birds of great speed as the wild goose. There are also gradational forms between the two extremes. Nor are these two methods confined to the birds, for among the pterodactyls it is evident that both kinds of true flight prevailed. Also, among the bats there are some of rapid wing movement, while others flap slowly, tending toward the sailing method of flight.

While the mode of flight is perfectly apparent in most aërial vertebrates, in some instances it has been difficult to assign the animal to the proper group as in the case of flying-fishes whose method of locomotion has given rise to much argument. Moseley's description of the flight of the albatross (Moseley, '79, p. 570)

[1] I am not sure under which head the fossil flying-fishes should come; but unless their fin-wings were far larger proportionately than those of modern types Colonel Durnford's argument would hold good for them as well and would place them among the true fliers (*vide infra* p. 541).

is another instance of the correction of a popular misconception due to a lack of knowledge of mechanical principles, for while vultures, when sailing, are continually sliding down an inclined plane, the albatross was supposed to sail close to the sea without losing altitude; a manifest impossibility.[1]

Classification

Volant vertebrates may be classed as follows:—

Evolution			Soaring	Flapping	Sailing
	Pisces				
1	Ganoidei	Thoracopterus		×	
2		Gigantopterus		×	
3	Teleostomi	Exocœtus		×	
4		Dactylopterus		×	
	Amphibia				
5	Anura	Rhacophorus	×		
	Reptilia				
6	Squamata	Ptychozoön	×		
7		Draco	×		
8	Pterosauria	(entire order)		×	×
9	Aves	(entire class)		×	×
	Mammalia				
10	Marsupialia	Ptauroides	×		
11		Petaurus	×		
12		Acrobates	×		
13	Rodentia	Anomalurus	×		
14		Pteromys, Sciuropterus, Eupetaurus	×		
15	Insectivora	Galeopithecus	×		
16	Chiroptera	(entire order)		×	
17	Primates	Propithecus	×		
		Total	10	7	2

In all 17 evolutions.

[1] Moseley says: "I believe that Albatrosses move their wings much oftener than is suspected. They often have the appearance of soaring for long periods after a ship without flapping their wings at all, but if they be very closely watched, very short but extremely quick motions of the wings may be detected. The appearance is rather as if the body of the bird dropped a very short distance and rose again. The movements cannot be seen at all unless the bird is exactly on a level with the eye. A very quick stroke, carried even through a very short arc, can of course supply a large store of fresh momentum. In perfectly calm weather, Albatrosses flap heavily."

FISHES

The flying adaptation among fishes has occurred at least four times; twice among recent fishes and fully as often during geological times. Dr. O. Abel in the last *Year-book of the Austrian Geological Survey*, describes and figures two ganoid flying-fishes from the New Red Sandstone (Upper Trias). These are Thoracopterus and Gigantopterus and they differ totally from the modern types, except in the development of wing-fins for flight. They

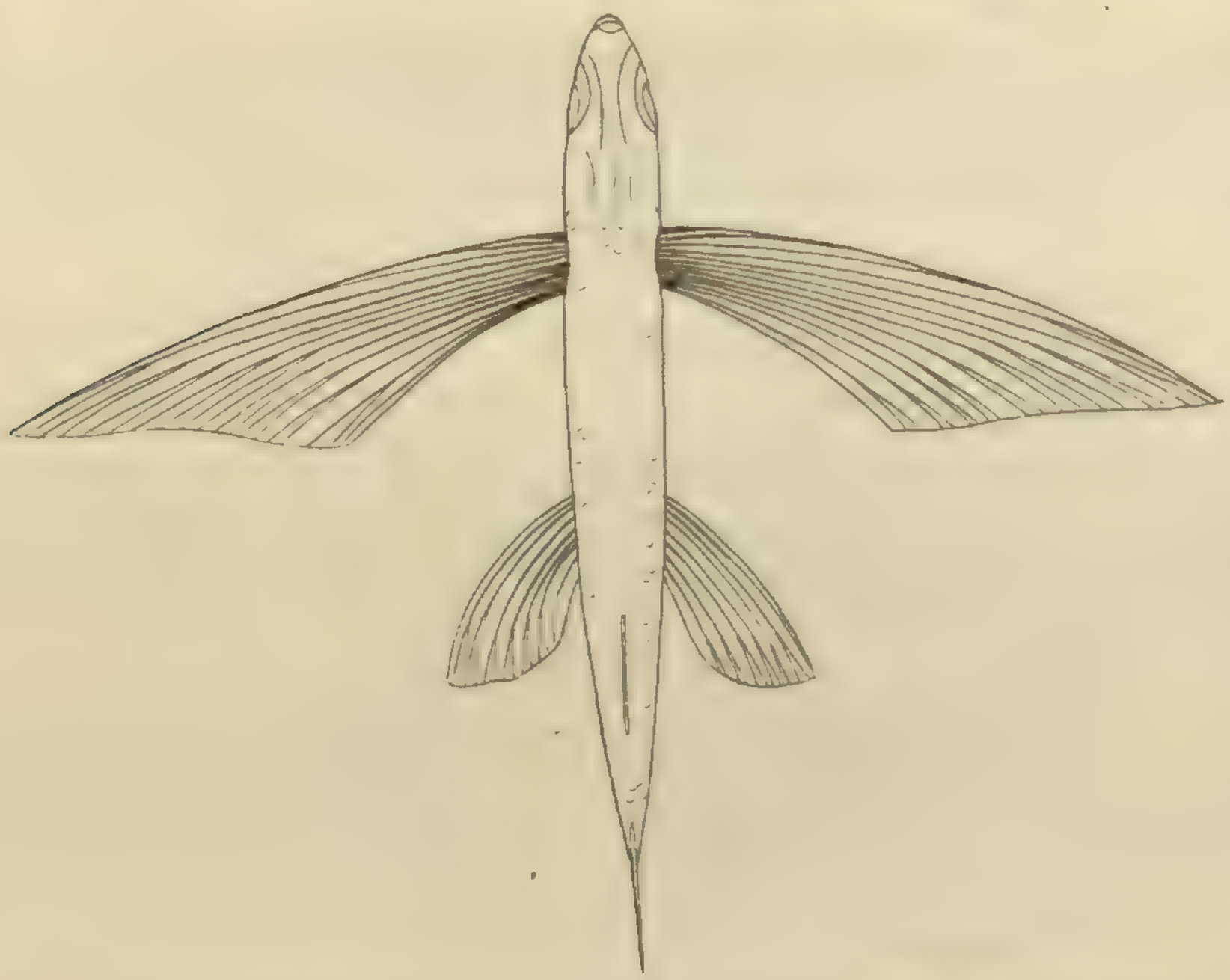

FIG. 1.— *Exocœtus* sp., drawn from an alcoholic specimen. ¼ natural size.

resemble their non-flying contemporaries in the possession of quadrangular, enamel-covered scales which encased the body.

Of modern types two important genera of Teleostomi have acquired flight, Exocœtus, a herring, and Dactylopterus, a gurnard.

Exocœtus.— This genus embraces forty-four species which are generally known as the true flying-fishes in contradistinction to the flying-gurnards or gurnets mentioned above.

In Exocœtus flight modification consists in the elongation and broadening of the pectoral fins and a lesser enlargement of the pelvics as well; so that the weight while in the air is distributed, though unequally, between the two sets of fins as shown in Fig. 1. The anterior fin-rays are much strengthened, especially toward

their base, while distally each ray bifurcates to give more support to the flying membrane. The lengthening of the pectoral fins varies with the species, being greatest in those with the best powers of flight.

The bodily contour seems to have suffered but little alteration due to the development of flight. The lower lobe of the caudal fin is much the longer and thus becomes more efficient in giving the fish its final impetus upon leaving the water. It is also said that the fin is occasionally submerged during flight and aids in changing the direction of the fish.

Nearly all of the Scombresocidæ, to which family this flying-fish belongs, have the power of taking great leaps out of the water, culminating in Exocœtus. In the development of the pectoral fin every gradation may be found between the small pectorals of Scombresox to Exocœtus, Hemiexocœtus being a very remarkable connecting form (Boulenger).

Exocœtus is tropical to subtropical in distribution, some species having an extremely wide range.

The manner of the flight of flying-fishes has been a much vexed question, one idea being that the creature gets its impetus solely from the tail while in the water, the wings acting merely as parachutes or aëroplanes to support the animal in the air. The other view is that while the initial start is given by the tail, flight is sustained by an actual vibration of the fins as in wing-flapping birds and bats. Some authorities have maintained that the fins move voluntarily only at the beginning and end of the flight, others that this apparent movement is due to an occasional vibration caused by the currents of air.

Colonel Durnford in the January number of the *American Naturalist*, has effectually settled the question by showing that sustained soaring for such a distance (500 feet, Günther) is a mechanical impossibility, due to the moderate initial speed, for a creature of such limited wing-area in proportion to its weight. He further shows that not only is wing vibration necessary, but vibration at extreme speed, such as is invisible to most eyes except at the beginning and end of the flight when the fins are accelerating or retarding their velocity. This is in spite of the statement of Möbius ('78, p. 343) who after examining the musculature as well as watching

the living fish came to the conclusion that the fins are not moved at all.

Dactylopterus.— In Dactylopterus the pectoral fins are especially developed for flight and they alone give support to the body in the air as the pelvic fins, which are situated just beneath the pectorals, are not visible from above even when extended. The pectoral fins as a compensation are much broader than in Exocœtus, the relative alar expanse compared with the bulk of the body being much the same in the two genera (compare Figs. 1 and 2).

In the present form the entire body is heavier and of more robust

FIG. 2.— *Dactylopterus volitans.* From an alcoholic specimen. ¼ natural size.

build and the strongly armored head is flattened beneath. The tail in Dactylopterus is symmetrical, not with a larger lower lobe as in Exocœtus.

The pectoral fins, aside from their greater breadth, differ from those of the latter genus in having more membrane in proportion to the supporting fin-rays, making a less rigid organ. In the young flying-gurnards, formerly thought to represent a distinct genus, Cephalacanthus, the pectorals are so much shorter than those of

the adult that they are unable to raise themselves out of the water (Günther).

Moseley ('79, p. 571) says: "I have distinctly seen species of Flying Gurnets move their wings rapidly during their flight .... especially in the case of a small species of Dactylopterus with beautifully coloured wings, which inhabits the Sargasso Sea." He further says that he has never seen any species of Exocœtus flap its wings which must be taken as indicating that in Dactylopterus the movement is much slower so as to be distinctly visible. This one would be led to expect from the feebler wing structure and the result is a much less developed power of flight. Moseley likens the flight of the gurnets to that of grasshoppers.

Boulenger (:04, p. 701) recognizes four species of Dactylopterus which are found in "the tropical and warm parts of the Atlantic and Indian Ocean and Archipelago."

Amphibia

The only volant adaptation among the Amphibia is that of the tree frog, Rhacophorus, in which the webbed feet bear the creature

Fig. 3.— *Rhacophorus rheinhardtii.* After Duméril and Bibron. Natural size.

up during the prolonged leaps that it takes from tree to tree.

This genus includes more than forty species and has a wide dis-

tribution in the paleotropical realm. It was first described by Wallace ('69, p. 38) who evidently through error exaggerated the extent of the supporting membranes very much. The generic name is derived from the presence of the small dermal flaps seen especially at the heel.

The digits terminate in adhesive pads and are connected by web-like expansions of skin which also extends between the two outer metatarsals. Membranes are developed as well in front and behind the arms, rudiments of the prepatagium seen in higher forms.

The figure (Fig. 3), which is modified from that of Duméril and Bibron ('36, pl. 89), is that of *Rhacophorus rheinhardtii* and shows a very conservative development of the parachute, though in the majority of species the web extends not more than half the length of the fingers. In *Rhacophorus pardalis* the total alar expanse is about three square inches (Gadow). This would imply rather feeble soaring powers.

REPTILIA

Reptilia exhibit at least three instances of volant adaptation, the most notable instance being that of the extinct Pterosauria in which

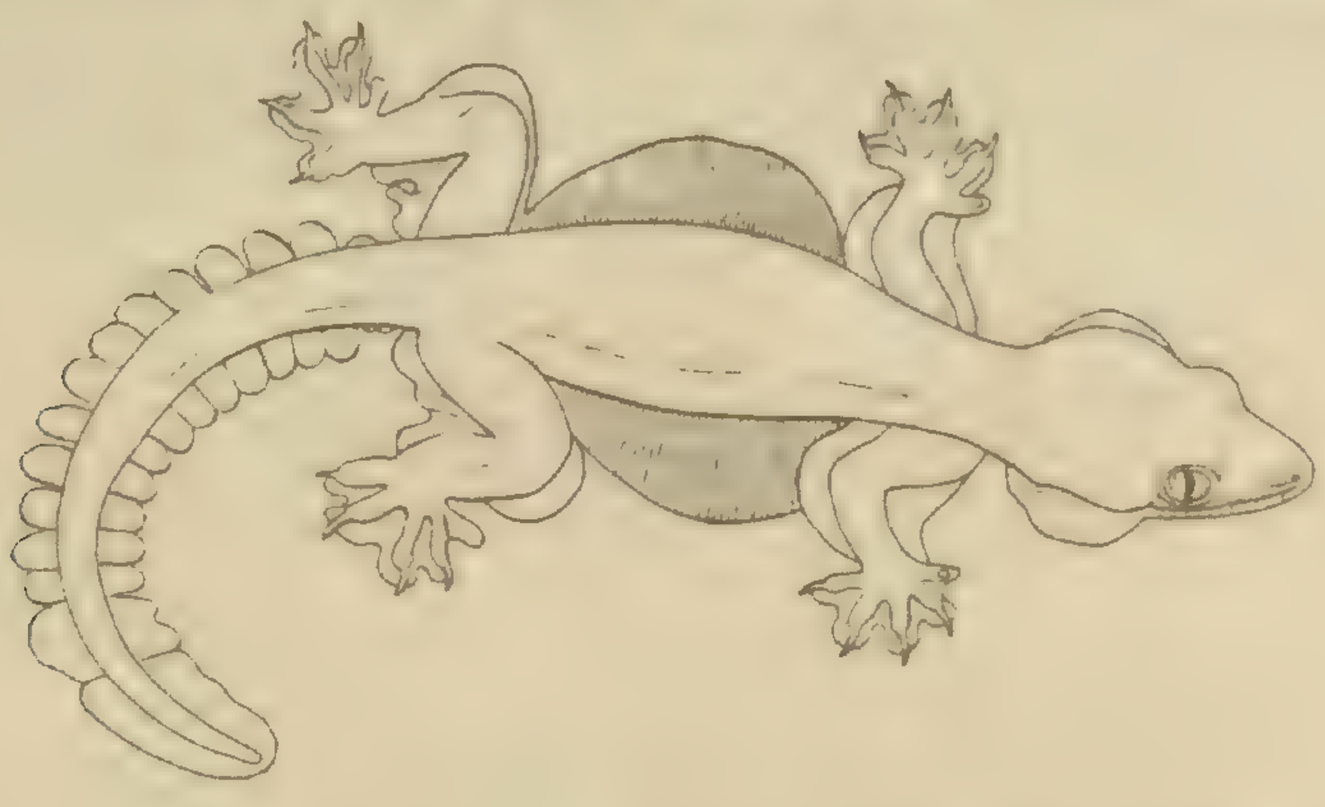

FIG. 4.— *Ptychozoon homalocephalum*. After Duméril and Bibron.

true flight was developed, the special adaptation of the entire organism being second only to that of birds.

Lacertilia.— Among modern types two lizards have the power of soaring, though in varying degree.

Of these lizards the first is of the family Geckonidæ, *Ptycho-*

zoön homalocephalum, a remarkable form from the Malay Islands and the Malay Peninsula. This creature, shown in Fig. 4, is about eight inches in length, a typical gecko in foot structure, but with membranous expansions along the sides of the head, limbs, body, and tail. The membrane also extends between the digits as in Rhacophorus. The membrane of the tail consists of a series of short flaps on either side. These extensions of the skin seem to be unsupported in contrast to those of Draco, but subserve the same function of supporting the creature in its soaring leaps.

The membranes are discernible in the newly hatched young (Gadow).

In *Draco volans* of the family Agamidæ, the supporting membrane is limited to the sides of the trunk and is of ample extent, well supported by the ribs of which five or six pairs extend beyond the body wall as shown in Fig. 5. The membrane is capable of being closed like a fan against the sides of the body, and its efficiency as a buoyant organ is increased by the concavity of the inferior surface.

FIG. 5.— *Draco volans*. From a mounted specimen. ½ natural size.

The body is strongly depressed and the tail is extremely long and slender and must aid the creature in guiding its flight.

There are in all about twenty species of Draco, inhabiting the East Indies. The power of flight is not very great, but probably exceeds that of Ptychozoön.

PTEROSAURIA

The pterodactyls were a remarkable group of reptilian forms whose remains are known from the Mesozoic rocks, ranging from the Rhætic to the Upper Chalk. As yet we know nothing of their ancestry, for the first which appear are in every way characteristic of the group.

Seeley (:01, p. 229) says: "There is no geological history of the rapid or gradual development of the wing finger, and although the wing membrane may be accepted as the cause of its existence the wing finger is powerfully developed in the oldest known pterodactyls as in their later representatives.

"Pterodactyls show singularly little variation in structure in their geological history. We chronicle the loss of the tail and the loss of teeth. There is also the loss of the outermost wing-digit from the hind foot as a supporter of the wing membrane. But the other variations are in the length of the metacarpus, or of the neck, or of the head." One might add to this an increase of size as the huge pterodactyl Pteranodon and its allies are among the last to appear.

The adaptation of the pterodactyls for flight is a very perfect one, implying not only the development of true wings, but a specially modified respiratory apparatus coupled with a highly developed pneumaticity of the bones as in birds. There is also a very bird-like modification of the brain which is unlike that of any other reptile. This is seen especially in the width of the hemispheres which touch the well developed cerebellum. On each side of the cerebellum lie the optic lobes while the flocculi, lateral appendages of the cerebellum, which are known elsewhere only in birds, are well developed (Gadow).

Skull.—The skull resembles that of birds, exhibiting large vacuities in some forms and bearing well developed teeth set in distinct sockets and varying in size. In Pteranodon and its allies the jaws were toothless and were evidently not sheathed with horn but with a leathery skin, indicating probably fish-eating habits. Posteriorly, the skull of Pteranodon is prolonged into a compressed,

vane-like process evidently not for muscular attachment but to aid in keeping the head pointing into the wind. This would otherwise not only require great muscular effort but would probably have deflected the creature from its course. The head is articulated at right angles with the neck as in birds and in bipedal dinosaurs.

Wings.— The wings consist of the patagium, a broad expanse of membrane, supported by the fore and hind limbs, a prepatagium in front of the arm, and an interfemoral membrane extending between the hind limbs and the tail. The patagium was delicate and very similar to that of the bats. The surface was marked with delicate striæ, which seem to be minute wrinklings. The membrane, when not extended, was thrown into longitudinal folds.

Fore Limb and Girdle.— The skeleton of the fore limb and girdle

FIG. 6.— *Rhamphorhynchus phyllurus.* Modified from Marsh and Zittel. About ⅓ natural size.

shows a remarkable modification for the purposes of flight, differing markedly from either the bird or the bat. The pectoral arch is reduced to two pairs of elements, the scapulæ and coracoids, as the clavicles are entirely wanting. In the forms existing before the Cretaceous period the scapulæ are saber-shaped and are united with the coracoids at an angle of less than 90° exactly as in carinate birds. The Cretaceous pterodactyls differ, however, in that the scapulæ, while articulating at right angles with the coracoids, are directed toward the vertebræ uniting with their neural arches. In Pteranodon the scapula articulates with the coalesced spines

of several coössified vertebræ, being, as Marsh says, "virtually a repetition of the pelvic arch, on a much larger scale" (Marsh, '82, p. 254).

The sternum is large with a carina or keel, especially in the anterior part, which extends forward in front of the coracoid articulations. The keel is but feebly developed in the great sailing forms like Pteranodon while on the other hand it is very high in Rhamphorhynchus which evidently flew by flapping the wings rapidly. The coracoids unite with the sternum by a true synovial joint.

The most notable feature of the humerus is the form of the proximal articular surface which is saddle-shaped, being concave along the horizontal axis and convex vertically. There is also a remarkable development of the radial crest.

The ulna and radius are nearly of the same size, the latter being

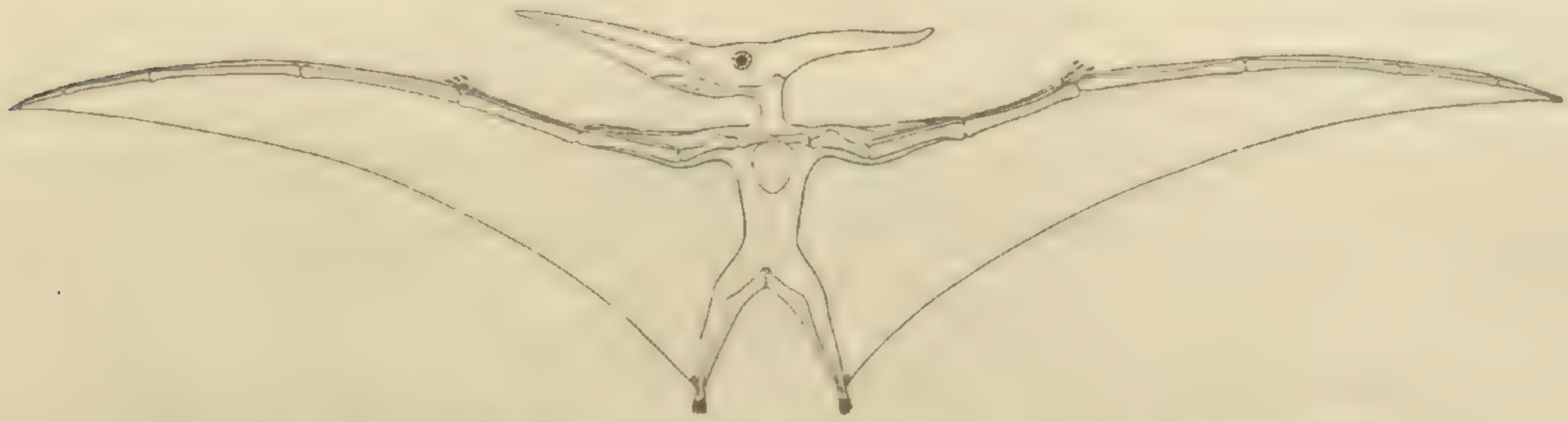

FIG. 7.— *Pteranodon* sp. Modified from Eaton. About $\frac{1}{24}$ natural size.

somewhat smaller, while of the metacarpals, that of the wing finger is of great size and strength while those of the three preceding digits are very slender bones. The joint for folding the wing is between the metacarpals and phalanges, not at the wrist as in birds.

The number of digits is probably five as there are two bones articulating with the distal carpal on the inner side of the wrist which Marsh ('82, p. 254) interprets as the metacarpal and first phalanx of the first digit. The phalanx, which he calls the "pteroid bone," formed part of the support for the prepatagium, being directed inward toward the shoulder. Others have interpreted this bone as an ossified tendon. If Marsh is correct the number of digits would be five, the fifth being the wing finger.

Hind Limb and Pelvis.—The pelvis is crocodilian in character, while the hind limbs are bird-like with splint-like fibulæ and long, slender tibiæ. The feet have long metatarsals bearing five digits.

In Dimorphodon and other long-tailed forms the outer digit resembles somewhat that of the hand, only on a much smaller scale. It probably also aided in the support of the patagium. In the short-tailed types, on the contrary, this digit is reduced to a vestige without phalanges.

I have figured for comparison two notable genera, the types of which may each be found in the Yale University Museum. Of these, Rhamphorhynchus, representing the suborder Pterodermata Seeley, is a small form from the Solenhofen Slate with a long tail terminating in a peculiar vertical rudder-like expansion supported by neural spines above and by the chevron bones below. This was undoubtedly for steering (Fig. 6).

The other form, Pteranodon (Fig. 7), belongs to the suborder Ornithocheiroidea of Seeley. It is from the Kansas Chalk, a creature with an alar expanse of eighteen feet! Vast in comparison with the diminutive body. In Pteranodon the tail is reduced to a vestige which afforded but little support to the interfemoral membrane. If one may judge from the relation of wing expanse to the size of the body it would seem as though Pteranodon must have had a sailing flight, flapping the wings slowly if at all. It may have been similar to the albatross (*vide supra*, p. 539) in habits of flight, or it may have been unable to fly except on a windy day when, by facing the wind, it would be able to rise to a considerable altitude before its inertia was overcome. Rhamphorhynchus on the other hand was probably a more active flier exhibiting the wing-flapping method of flight.

Birds

The birds form a remarkably homogeneous group reaching the climax of volant adaptation. Flight has, however, been lost in some of the more specialized forms as the penguins among the Carinate birds and in the whole group of so called Ratite birds.

In brief, the modifications for flight consist in the alteration of the fore limb into a wing with a reduced hand and with slightly developed pre- and postpatagiums, but with the alar expanse increased by the development of the feathers. The tail also becomes an

efficient steering organ and adds materially to the support of the animal in the air as well. Aside from the bodily conformation which is such as to offer but little resistance to the air in passage, the respiratory organs seem to show the best adaptation to its mode of life of all the other mechanisms of the bird.

A very interesting series of comparisons may be made between the birds and the pterodactyls which must be explained as the result of convergence, though the evidence of a common ancestry for the two groups is very strong. Other characters there are in common with the dinosaurs, explicable in the same way, but these can hardly be said to be volant adaptations as we have no evidence that the dinosaurs acquired flight.

Fore Limb and Girdle.—The fore limb and shoulder girdle are wonderfully adapted to their purpose. In the pectoral arch all three elements are represented in contrast to the coracoid and scapula in the pterodactyls and the clavicle and scapula in the bats. The clavicles have united ventrally to form what is technically known as the furculum which does not always articulate with the sternum. The scapulæ and coracoids fuse with each other firmly, forming in the Carinatæ an angle of less than 90° as in the earlier pterodactyls, while in the Ratitæ the angle formed is greater than 90°, a feature associated with the loss of flight.

The scapula is saber-shaped, and lies parallel with the vertebræ, with which it never articulates as in the later pterosaurs. The coracoid is a massive, pillar-like bone firmly articulated with the sternum. Its duty is to withstand the stress of the great pectoral muscles which would pull the shoulder toward the breast-bone were it not for the resistance offered by the coracoid.

The sternum is large, covering in the Carinatæ much of the ventral wall of the chest and it bears along its midventral line a high keel or carina for the origin of the muscles of flight. In the Ratitæ the keel is wanting, having been lost with the reduction of the pectoral muscles. In pterodactyls the sternum is similarly keeled, though to a less extent, in the smaller forms which had flapping flight. The keel becomes obsolete except upon the forwardly projecting process of the sternum in such huge forms as Pteranodon which, as we have seen, were probably sailers.

In the carinate birds the humerus is notable mainly for the size of the crests which afford attachment for the various muscles. The humerus is reduced in those birds which have lost the power of flight and may be entirely absent as in many of the moas.

Seeley (:01, p. 47) tells us of the remarkable similarity which exists between the foramen in the humerus of the pterodactyl and that of the bird, by which air enters the cavity of the bone. He says: "In the Pterodactyle the corresponding foramen has the same position, form, and size, and is not one large hole, but a reticulation of small perforations, one beyond another, exactly such

FIG. 8.— *Archæopteryx macroura.*

as are seen in the bone of a bird in which the pneumatic character is found."

There are in modern birds but three unequally developed metacarpals which are firmly coössified. The digits are represented by one, or rarely two, phalanges in the pollex which supports the bastard wing, while the second digit, which is much the largest, bears two, and the third one phalanx. Claws are sometimes borne on

the first and second digit in modern birds; in Archæopteryx upon the third as well.

Archæopteryx exhibits naturally a more primitive condition of structure than do modern birds, but even here the features are truly bird-like. The sternum is not well known, but the furcula and the coracoids are like those of existing birds. The wing is shorter in Archæopteryx with rather slender bones; the humerus is somewhat longer than the radius and ulna. But one carpal bone is known though at least one other must have existed. The three metacarpals are free and each bore a well developed digit terminating in a claw. We do not know whether the second bore any of the contour feathers as in modern birds or whether they were all borne on the third finger.

Hind Limb and Pelvis.— The hind limb and pelvis of birds can hardly be said to exhibit volant adaptation, unless it be in the development of pneumaticity, as their structure is so closely paralleled in certain of the dinosaurs. It seems rather that the dinosaur-avian type of limb, or the tendency to acquire it, is an inheritance from a common ancestor which certainly could not have possessed the power of flight as the dinosaurs show no evidence of having had and lost this characteristic.

Tail.— The tail of the bird shows a distinct flight modification less developed, however, in Archæopteryx in which the tail was elongated and lizard-like and bore a pair of oppositely placed feathers on each segment. These evidently were used for steering and must have afforded a good deal of support to the body as well, in compensation for the comparatively small wings. The Neornithes or modern birds, on the other hand, have shortened tails, several of the terminal vertebræ having fused to form a pygostyle. Around this vestigial tail the rectrices are arranged fan-wise making a very efficient organ for steering and for checking the rapidity of flight.

A comparison of the figure of the pigeon (Fig. 9) with that of Archæopteryx (Fig. 8) is interesting as showing the increase in the expanse of the wings to compensate for the reduction of the tail so that the relative buoyant surface remains approximately the same.

The Trunk.— The rib structure of the Neornithes must be considered as a definite flight modification for here only do we find the

sternal and vertebral ribs articulating by a true synovial joint. This, together with the elbow-like flexion of the joint, forms an admirable mechanism for the dorso-ventral increase and decrease of the chest cavity during respiration. When the bird is resting the back is rigid and the sternum moves, but during flight when the sternum is supporting the creature it is the back which rises and falls.

The long slender neck and the tendency on the part of the trunk vertebræ to coössify, are further skeletal characteristics of birds.

Respiratory Organs.— While all of the nutritive organs are necessarily larger and more efficient in birds as the direct result of more

FIG. 9.— *Columba livia*. Modified from Parker and Haswell.

rapid expenditure of energy during flight, the respiratory organs show the most remarkable adaptation. The lungs are inelastic and do not hang freely in the cavity of the chest as do those of mammals, but are connected with an extensive series of air sacs, principally in the abdomen, but in other portions of the body as well. These serve not only to lighten the specific gravity of the bird, but, by means of the abdominal sacs, air is drawn *through* instead of merely into the lungs with the result that the air in the latter is entirely renewed with each inspiration. There being thus no residual air, the entire lung functions for the aëration of the blood. The respiratory system is further connected with the cavities within the bones as in pterodactyls and while this pneumaticity is evidently an aid to flight as it reaches its maximum development in such powerful fliers as the pelicans, it is on the other hand but little

developed in the gulls which are also strong of wing. Seeley says: "Comparison shows that in so far as the bones are the same in the bird and ornithosaur, the evidence of air cells entering them extends to resemblance, if not coincidence in every detail. No living group of animals except birds has pneumatic limb-bones, in relation to the lungs; so that the identical structures in the bones were due to the same cause in both living and extinct groups of animals" (Seeley, :01, p. 50).

Brain.— In the avian brain the convergence[1] toward that of the pterodactyl lies in the position of the optic lobes which are laterally displaced so that the cerebrum may extend between as well as over them in order to abut against the cerebellum. There is also a similarity in the development of the lateral lobes or flocculi upon the sides of the hind brain. These features seem to be adaptations correlated with the development of flight.

MAMMALIA

The Mammalia show at least eight distinct flight evolutions. In seven instances soaring has been developed as an aid to prolonged leaps, while the Chiroptera as an order are true fliers. This should not surprise us for all but one of the forms are arboreal and with arboreal types the development of parachutes for sustaining the creature in the air during its passage from tree to tree is a logical course of evolution.

Marsupialia

Among the marsupials of the family Phalangeridæ there are three genera, Petauroides, Petaurus, and Acrobates, which have independently acquired the power of soaring; for the three genera are each in turn especially related to a separate type of non-flying phalanger. The same observation can be made about the flying squirrels, Anomalurus and Sciuropterus (Beddard).

[1] Dr. F. B. Loomis is of the opinion that the brain similarity is due to real relationship and is not a convergence. He explains in the same way the similarity of the openings into the pneumatic bones.

In all of these forms the flight adaptation consists mainly in the development of a horizontal fold of skin (the patagium) stretched along the sides of the body between the fore and hind limbs.

Petauroides.— In Petauroides the flying membrane extends from the wrist to the ankle, but is very narrow along the lower segment of each limb. The tail is very bushy except for its prehensile tip which is naked inferiorly, and, together with the long fur which clothes the body, must aid considerably in buoying the creature up while soaring.

Petauroides includes but a single species, *P. volans*, the so called Taguan flying phalanger, found in Australia from Queensland to Victoria. Its nearest ally is Dactylopsila which, however, has no flying membrane but has the same partially naked tip to the tail.

FIG. 10.— *Petaurus sciurius*. Modified from Flower and Lydekker.

Petaurus.— Petaurus has a much broader patagium which extends from the outer finger to the tarsus; there is also a slight extension of membrane in front of the fore limb. The tail is very large and evenly bushy, lacking the naked tip. This genus contains three species which are somewhat smaller forms than Petauroides. They seem to have been derived either from the genus Gymnobelideus, which resembles Petaurus closely except that it is flightless, or from an allied extinct form (Lydekker).

The geographical range of Petaurus is "over New Guinea and part of Australia, including the area from the Halmahéra group of Islands to Victoria."

Acrobates.— The third genus, Acrobates, contains two species of which the individuals are of small size with a narrow patagium extending from the elbow to the knee along the flank. The buoy-

ant area is increased, however, by the long fringing hairs. There are striated pads at the extremities of the digits. The probably prehensile tail has its long hairs arranged on either side as in its near ally, the pen-tailed phalanger, Distæchurus, which from its skull and teeth may be very close to the ancestral type of Acrobates.

One species, *Acrobates pygmæus*, is found in Queensland, New South Wales, and Victoria and the other, *A. pulchellus*, in Papua, while Distæchurus is now found in New Guinea. Acrobates is extremely active with great soaring powers.

Rodentia

Two families of rodents, the Anomaluridæ containing but one flying genus Anomalurus, and the Sciuridæ containing among others the flying genera Pteromys, Sciuropterus, and Eupetaurus, have developed the power of soaring by means of a patagium.

These families represent in each case a distinct adaptation to volant life, though the three genera of the Sciuridæ are closely related and are not as in the Phalangeridæ, related each in turn to a non-flying ally. The convergence of the flying rodents toward the flying phalangers is very marked though the former are apt to develop more or less of a prepatagium and an interfemoral membrane in addition to the patagium along the flanks. This is, however, as will be shown, a variable feature.

Anomalurus.— The Anomaluridæ include three genera of which Anomalurus with six species is the most important. In this genus the patagium is well developed and is supported by a cartilaginous process of the olecranon. The membrane extends from the carpus to the tarsus but narrows along the front of the leg from the knee down. This is compensated for by an interfemoral membrane from the heel to the tail a little beyond its base.

A distinctive feature of these forms, while not a volant adaptation but rather an arboreal one, is the presence of imbricated, keeled scales beneath the tail which apparently aid in climbing. The tail is not very bushy so that it probably aids but little in flight.

Anomalurus resembles Pteromys but is distinguished therefrom

and from Sciuropterus by the caudal scales and by the position of the supporting cartilage. Anomalurus is African in habitat.

The allied genus, Idiurus, differs in minor details from Anomalurus, while Aëthiurus from the French Congo, has no flying patagium.

Pteromys.— Among the Sciuridæ, Pteromys has a patagium extending as far as the digits and supported as in Anomalurus, by a cartilage, but one arising from the carpus rather than from the

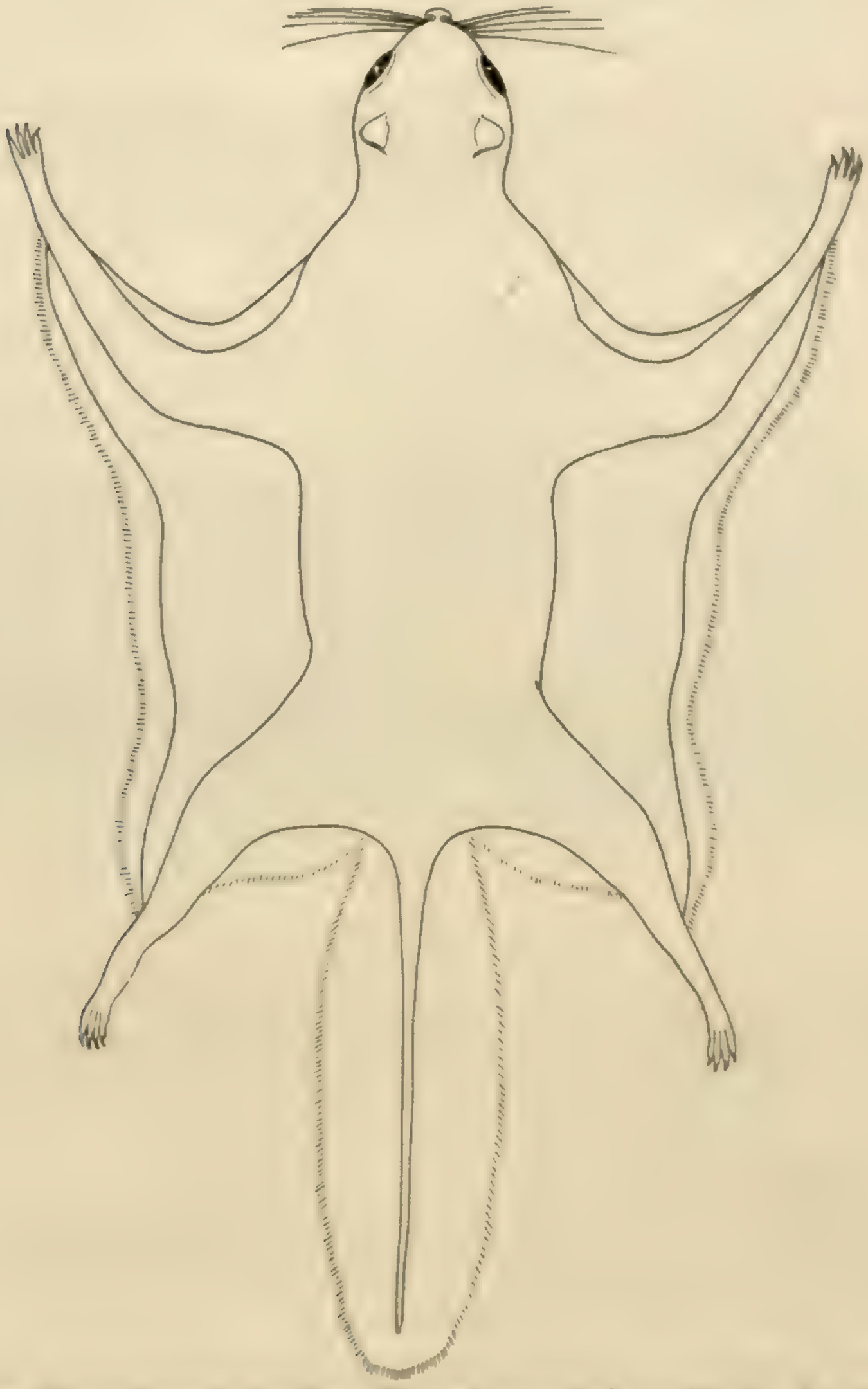

FIG. 11.— *Sciuropterus volucella.* From a mounted specimen. ½ natural size.

olecranon. In addition to the interfemoral membrane extending to the root of the tail, there is also a narrow prepatagium running from the anterior limb to the sides of the cheeks. The tail

is larger than in Anomalurus and must add materially to the support of the body in the air. It is said that Pteromys can soar through a distance of nearly eighty yards, depending of course upon the initial altitude above the ground.

Pteromys is found in the "wooded districts of tropical southeastern Asia, Japan, and some of the Malaysian Islands" (Heilprin).

Sciuropterus.—Sciuropterus, which is here figured (Fig. 11), has no interfemoral membrane, but as a compensation, the tail is much more fully developed than in Pteromys. In the latter it is round and comparatively thin while in Sciuropterus the tail is flat and broadly expanded. A hairy fringe extends beyond the margin of the patagium and behind the femora as well, thus extending the supporting area as the figure clearly shows.

Sciuropterus includes smaller forms than Pteromys, but its range is much more extensive as it includes the northern part of North America and the Eurasian continent.

Eupetaurus.—Eupetaurus resembles Pteromys but has no interfemoral membrane. It differs from the preceding forms mainly in having hypsodont teeth rather than brachyodont which implies a difference in feeding habits. Eupetaurus is rock- and precipice-inhabiting rather than arboreal and inhabits the high elevations of northwestern Kashmir.

Insectivora

Among the Insectivora, Galeopithecus stands alone in its volant adaptation for it shows the greatest specialization for flight of any of the Mammalia except the bats. Indeed Galeopithecus, while too specialized to be ancestral to the Chiroptera, is evidently from a common stock and gives us a pretty clear idea of the characters of the forms from which the latter arose.

In Galeopithecus, which is an animal of considerable size, the patagium is well developed and is supplemented by a prepatagium and an interfemoral membrane which includes the entire tail precisely as in the insectivorous bats. The patagium is well supplied with muscles and nerves which are homologous with those in the

wing membrane of the Chiroptera and differ decidedly from those of the other volant Mammalia.

The hand is much larger than the foot and the flying membrane is continued along the side of each as well as between the digits, and while the fingers show no trace of the elongation so characteristic of the bats, if such were to occur the result would be a very bat-like structure.

Galeopithecus is unique in the character of the teeth which are adapted to a phytophagous or leaf-eating habit, while the alimentary canal resembles that of the Chiroptera except that in Galeopithecus the colon is long, while in bats as in birds the colon is very short. This shortening of the colon is clearly a volant character due to the freedom with which excrement may be voided by

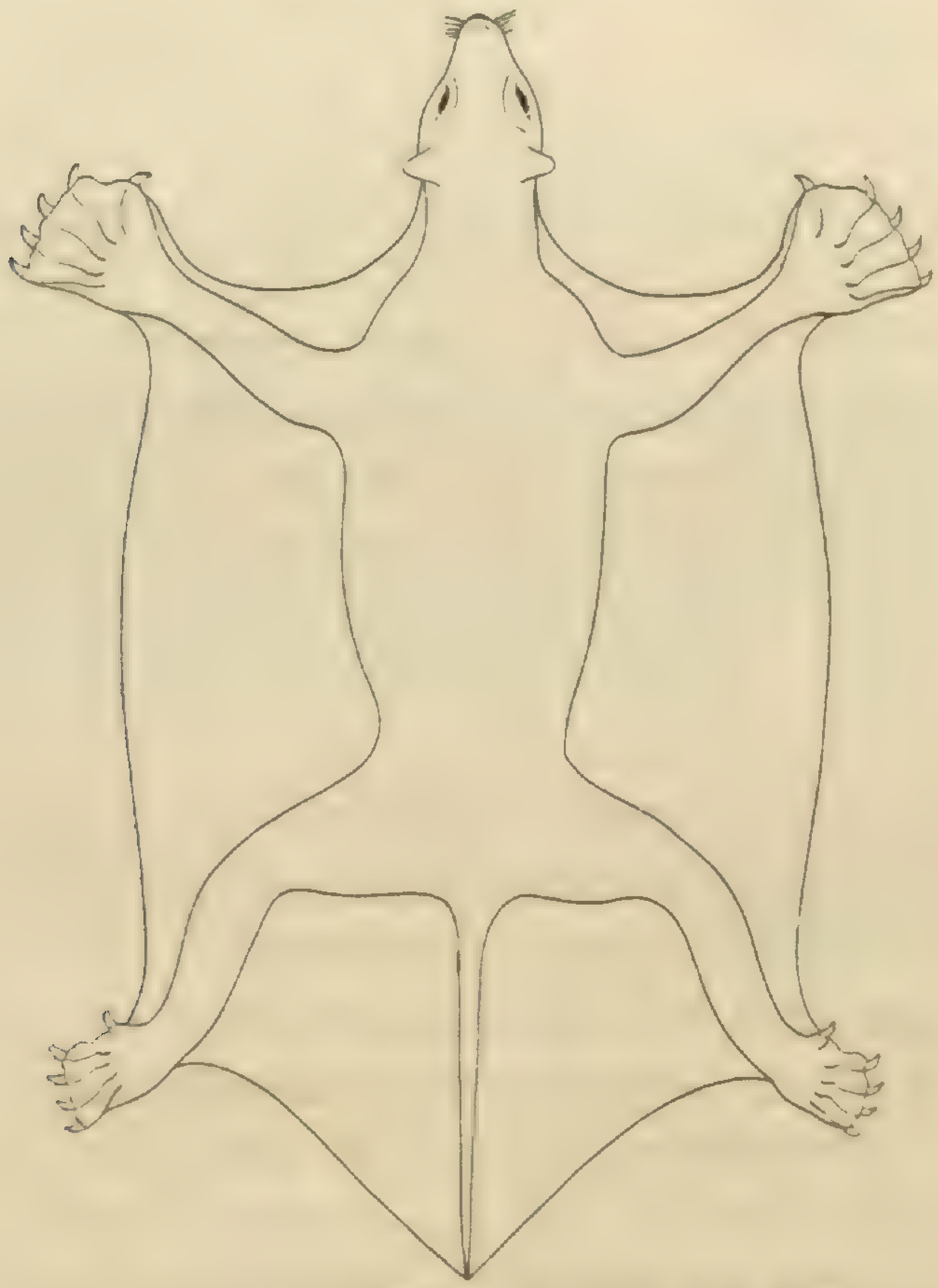

FIG. 12.— Galeopithecus. Modified from Wood.

aërial forms and the consequent lack of necessity for a place of storage of effete matter.

The brain in Galeopithecus is midway in its development between that of a typical insectivore and that of a bat.

Galeopithecus is nocturnal in habits, as indeed almost all volant mammals are, resting during the day by clinging head downward from the branch of a tree, in which posture it resembles Pteropus very closely. Its soaring powers are very great as one has been seen to cover a space of seventy yards with a descent of not more than thirty-five or forty feet, or less than one in five (Wallace).

Two species of Galeopithecus are known, one, *G. volans*, from the Malay Peninsula, Sumatra, and Borneo, while *G. philippinensis* inhabits the Philippine Islands.

Chiroptera

In the bats one sees the culmination of volant adaptation on the part of the Mammalia and the entire order has reached a state of perfection excelled only by the birds and pterodactyls. Each of the three solely air-breathing classes of vertebrates has, in one line of evolution at least, culminated in perfect adaptation to aërial life.

The bats while showing the same general plan of structure throughout, are divisible into two distinct suborders in which constant distinguishing characters have arisen, due to differences of habits. These are the Microchiroptera and the Megachiroptera the former being in the main insectivorous while the latter are frugivorous in habits. Each group, however, contains some aberrant forms.

The Patagium.—The most notable volant characters are the great development of the digits of the hand supporting the patagium which extends along the sides of the body and hind limb to the tarsus. There is a well developed prepatagium extending from the neck to the wrist. An interfemoral membrane is also present, but varies in development in the two suborders, including the somewhat elongated tail in the Microchiroptera, while in the tailless Megachiroptera each membrane is a triangular area meeting its fellow at the end of the spine. In the Microchiroptera the membrane is further supported by a cartilaginous rod, the calcar, arising from the heel and directed obliquely inward toward the tip of the tail. The development of the tail gives, with the interfemoral

membrane, an efficient organ for steering and checking the way of the animal during flight, so necessary in the pursuit of insects and which gives to the twilight bat its characteristic flight. It is also said that this structure is of use in the capturing of prey.

In the vampire and other aberrant carnivorous Microchiroptera, there is no tail, a point of agreement with the frugivorous forms. The tailless bats are much heavier fliers as a rule, flapping their way slowly through the air.

The patagium is naked, being clothed with hair along the sides

FIG. 13.— *Vespertilio noctula*. Modified from Flower and Lydekker.

of the body only, and the surface of the integument is finely wrinkled as in the pterodactyl Rhamphorhynchus. The method of folding the wing when at rest is also the same. The contrast between the wing of the bat and that of the pterodactyl is in the support of the membrane in the former by four digits, only the pollex being free, while in the latter the outermost finger alone supports the wing membrane. The contrast with the bird lies in the reduction of the digits in the latter to three and in the retrogression of the patagium whose place as a buoyant surface is taken by the feathers.

The Fore Limb.— The pollex is always free and clawed and aids in crawling on level ground, but more especially in climbing. In the Microchiroptera the second finger while distinct is not free but is attached to the third distally so that the two together support the anterior margin of the wing. The third finger, however, is much the longest and digits four and five are well developed and free.

In the Megachiroptera the contrast lies mainly in the difference in wing proportions due to the fact that the second digit is free from the third and supports a portion of the patagium alone. It is further clawed at the tip. A comparison of Figs. 13 and 14 will render these distinctions clear.

The bones of the wing are very slender with large medullary cavities, but without any trace of pneumaticity as in birds and pterodactyls. The shoulder girdle, consisting of well developed clavicles and scapulæ, is very strong. The clavicles are curved and the scapulæ bear strongly curved coracoid processes. The humerus is well developed but is much exceeded in length by the radius which is a strong, curved bone while the ulna is much reduced.

The Hind Limb.— One chiropteran peculiarity which is clearly a flight adaptation is the backward rotation of the hind limb so that the knee points towards the rear instead of toward the front as in quadrupeds. This feature is a distinct disadvantage for terrestrial locomotion, making the creature extremely awkward when upon the ground.

There are five compressed digits in the pes bearing long, curved claws and used as in Galeopithecus for suspending the creature head downward when at rest.

The Trunk.— The chest is remarkably capacious to contain the large lungs and heart which resemble those of birds in their state of development.

The vertebral column is short owing to the compact form of the body and the individual vertebræ have but little movement and tend to coössify in old age. The neural canal is largest in the cervical and thoracic regions, rapidly diminishing toward the rear. This is due to the large size of that portion of the spinal cord from which the great muscles of flight are innervated as contrasted with the feeble development of the posterior portion of the body.

The presternum has a well developed keel as in birds and pterodactyls for the origin of the muscles of flight.

The Brain and Sense Organs.— While the brain of the Chiroptera is of as lowly organization as the most nearly allied order, the Insectivora, certain senses of the bats, especially that of touch,

have undergone a remarkable degree of development and refinement. This tactile sense seems to reside mainly in the vibrissæ, in the wing membrane, and in the ear pinnæ which in some types are very large. More especially is the sense developed in the leaf-like expansions of the skin about the nose and face in the Rhinolophidæ and Phyllostomatidæ. These appendages are the seat of so delicate a sense of touch that actual bodily contact with an object

FIG. 14.— *Pteropus* sp. Modified from Owen.

is not necessary to its perception, but the reflected aërial waves suffice to stimulate the sense organ. This is a notable secondary flight adaptation, not useful as a direct aid to flight, but in guiding a rapidly moving nocturnal flier it must prove invaluable.

The Chiroptera are practically world-wide in distribution, being found wherever sufficient food may be procured.

Primates

Among the primates one genus exhibits a small patagium which aids in soaring. This is the genus Propithecus of the family Lemuridæ.

In these forms the power of flight is somewhat limited. Flower and Lydekker give ten yards as the length of the leap, attributing the soaring to the powerful hind limbs, without even mentioning the existence of the patagium. Beddard on the other hand speaks of the "parachute-like fold of skin between the arms and the body which suggests the more complete parachute of Flying Foxes, etc."

Propithecus includes three species, all from the Island of Mad-

agascar. They are diurnal, contrary to the general rule among volant mammals, though they prefer the morning and evening for their periods of activity.

Summary

1. Volant evolution has occurred seventeen times among vertebrates, ten of which are merely adaptations for more or less prolonged soaring leaps, while in seven instances in all probability true flight has been developed.

2. Soaring implies, with but one exception, the development of a fold of skin along the creature's flanks supported in one instance by the extension of the ribs beyond the body wall, but generally stretched between the fore and hind limbs. This fold is often supplemented by others in front of the fore limbs and between the hind limbs sometimes involving the tail.

3. True flight always implies a more or less profound modification of the fore limbs which become, as a consequence, unsuited to ordinary progression. True flight has been developed once in each of the classes of strictly air-breathing vertebrates, and probably at least four times among fishes.

4. With the exception of the fishes, soaring implies also present or ancestral arboreal adaptation and this may apply as well to the true fliers. It is certainly true of the bats, possibly true of the birds, but of the pterodactyls one cannot be certain.

5. Besides the primary modifications which constitute the machinery of flight, other portions of the body, especially the nervous system, the sense and the nutritive organs, may exhibit secondary volant characteristics. These, as with the primary modifications, are in direct proportion to the powers of flight.

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EXTERNAL MORPHOLOGY OF THE DUGONG

H. DEXLER AND L. FREUND

In continuation of our previous article in this journal on the physiology and biology of the dugong, we wish now to treat of its external morphology. Present knowledge of this subject is indeed considerably greater than that of its biology though it is still far from complete and particularly has the want of a good figure of the animal been felt. Kükenthal was keenly sensible of this and sought partially to remedy the defect by giving an excellent figure of a dugong embryo and its snout. It is our hope that the figures here given will at least in some degree make amends for this lack of illustrations, since they are from photographs taken by Dexler on the Australian coast during an expedition for the purpose of obtaining dugong material for scientific study, supported by the Gesellschaft zur Förderung deutscher Wissenschaft, Kunst, und Literatur in Böhmen. It is instructive also to compare these photographs with the first sketches of the dugong drawn from Nature by Dr. O. Finsch (*Illustr. Zeitung*, Leipzig, 1901, no. 3012). The description as well, is capable of improvement and amplification, for otherwise there would have been no object in obtaining the material.

As regards the size of the dugong, various measurements were made of several specimens killed and these measurements are here brought together in the following table.

Table of Measurements in Centimeters

No. and Sex	7♂	1♂	2♂	4♀	5♂	6♂	7♂
Total length	273	315	311	245	280	290	300
Greatest girth (hand's breadth behind flippers)				202	181	200	
Axillar girth						175	183
Breadth of caudal fin				77	82		77
Length of flipper				28	32	36	34
Breadth of flipper						20	22

No. and Sex	7♂	1♂	2♂	4♀	5♂	6♂	7♂
From eye to end of snout				18			
From eye to ear opening				15			
From anus to center of margin of tail				80	82		101
From genital opening to center of margin of tail				90	132		156
From navel to center of margin of tail					169		191
Interorbital width				21			
Width of snout				24	22		
Height of snout					17		
Depth of mouth cavity			10				
Palatal process (breadth: height)					7.4		
Extent of lung sounding (from tip of snout)					160		

From these measurements it is seen that the smallest specimen was a female, 245 cm. in length. The male animals obtained, measured from 280 to 315 cm. in length, and of these the two measuring 311 and 315 cm. respectively, were the largest of 25 dugongs captured. The published records of the size of these animals show some variation. Turner and Finsch have already pointed out that the older authors were wrong in placing the average length of the dugong much too high (*e. g.*, Brown, 20 feet), and indeed all the measurements examined show (*cf.* Raffles, Owen, Rüppel, Klunzinger) that the dugong does not exceed $3\frac{1}{2}$ meters in length (see also Finsch). In this, Rapp (8 to 10 feet) and Fairholme likewise agree. The statement of Brehm, 3 to 5 meters, is thus somewhat exaggerated. The length of the female is generally given as slightly less, and in our specimen was $2\frac{1}{2}$ meters (Owen, 2.23 m.; Klunzinger, 2.37 m.).

As to the color of the dugong, Finsch has previously written at some length, and has brought together the various expressions that have been applied to this elusive shade. His account and that of Gill appear to agree with our own observations, namely, that the dorsal surface is in general a light grayish brown to bright bronze-brown with a slight metallic shimmer, while the ventral side is white to bright gray. According to Finsch the younger animals are almost bright flesh-color. The color of the dugong of the Red Sea has been otherwise described (by Rapp, Rüppel, Brehm) as a dull lead-gray, the back and top of the head more greenish. The dugong embryos from Australia studied by Kükenthal were blue-black on the head and brown on the belly, and this

shade became lighter in larger animals. Brehm likewise mentions dark longitudinal streaks which, however, Kükenthal did not observe. Preserved skins become much darker with age until they are nearly black (Krauss, Finsch).

The skin is in general smooth, almost shining (Rüppel, Klunzinger, etc.). In case of animals that have been lying on the shore for some time, the skin, particularly of the dorsal side, shows an unusual luster. On the back and on the sides of the body there are numerous scratches and scars. These run in all directions, intersecting one another, and often are very deep, giving the animal a peculiar appearance. According to Klunzinger the dried skins show only a few scars but numerous furrows. Krauss also refers to the numerous scars and believes that they are due to injuries

FIG. 1.— Australian dugong, antero-lateral view.

from contact with the coral rocks. The back and sides of the body are thickly studded with Chelonobiæ and less numerous Balanus. Finsch and Brehm assert that the skin lies everywhere smooth and is wrinkled on the stomach only. According to Rüppel there are a few small longitudinal folds on the sides of the belly. On close examination, however, we find that the skin is really not smooth throughout, but that there are numerous furrows

and wrinkles particularly on the head and fore part of the body. Thus many of them run parallel to each other from the corner of the mouth between the upper lip and the eye. Others pass below the eye, to radiate out from in front of it. Between the eye and the ear are many transverse folds which run toward the base of the flipper. The nuchal region is likewise traversed by wrinkles, among them a particularly prominent neck furrow. Many others are present in the region of the eye and will be described in connection with the latter. A deep surface furrow is present at the junction of the flipper with the body, while dorsal to this, a broad band of fine wrinkles varying in width passes to the eye. A few deep furrows traverse the neck ventrally and pass caudally into numerous longitudinal folds. The navel, genital opening, and anus lie in these longitudinal furrows which in the old males are deeper and more numerous. Behind the anus are a few transverse furrows on the side and these Kükenthal found in the embryos as well.

All over the body in little pits stand the hairs, some of which are living, others dead. They are short and slender yet stiff bristles, and may readily escape notice on account of their distance

FIG. 2.— Dugong, lateral view. From sketch by Dexler.

from one another (Finsch) but by passing the hand over the back of the animal they may easily be felt. They are more numerous on the back than on the belly (Klunzinger). Their distance apart according to Krauss is from 0.5 to 0.8 cm., though these figures can hardly apply to an adult animal. For Kükenthal in an embryo the length of whose back was 72 cm., found the intervals between hairs to be from 4 to 8 mm. Rüppel gives the distance in adults as 1 inch, Brown as 1 to 2 inches, and according to our observations it is not much greater. In an embryo 162 cm. long, Küken-

thal found distances of from 2 to 3 cm. even at that early stage. This observer states particularly that there is a regressive development of the hairy covering in Sirenia such as he had shown previously to a greater degree in case of the Cetacea. Turner claims to have observed that the hairs were arranged in rows in an embryo dugong, but of such an arrangement we saw nothing. On the other hand, we found hairs, scattered to be sure, on the flippers and caudal fin where their occurrence is denied by Rapp, Rüppel, Brehm, and Finsch.

The body is in general spindle-shaped though not uniformly round as Rüppel and Brehm state. Anteriorly it diminishes in transverse diameter so that the head stands high, while posteriorly it decreases rapidly in vertical section till the body terminates in the horizontal caudal fin. The chest is somewhat trapezoidal in cross section in the middle, and toward the rear, with the decrease in width of cross section dorso-ventrally, it becomes flattened out laterally. The head is marked off by a shallow furrow at the neck. On the back the dorsal processes of the vertebræ are distinctly visible as low eminences all the way to the end of the tail as Owen has also shown. Rüppel noticed this feature in case of the tail only. The ends of the ribs also are evident along the sides of the breast.

The head of the dugong is the part showing the most modeling. The powerful curved upper mandible — compared by Brown to a nose of a very pronounced Roman type — the broad obtuse snout, and the nares situated on the summit of the head, give the latter a very characteristic appearance. We shall consider its peculiarities first through a study of the figures before going into the somewhat contradictory accounts in the literature of the subject. The head consists of a strikingly heavy skull and upper jaw and the small lower jaw almost lost to sight underneath it and separated from the cranium by the mouth cavity which slopes obliquely forward and downward. As before mentioned the head is marked off by a furrow at the neck. Ventrally, opposite the nape, a sharp clear boundary is made by a right-angled fold of skin. Seen from above, the head is longitudinally rectangular, considerably smaller than the neck, while the height of the head in side view is not greatly different from that of the neck. The top of the head

curves sharply down on each side to the eyes. Anteriorly, toward the nostrils this arching is very slight, corresponding with the decrease in width of this region. The crown of the head is without hair, whereas the remainder of the upper portion is set with transparent bristles, from 4 to 5 mm. long, that arise from dark-colored pits. The sides of the upper jaw fall away rather sharply from the summit of the muzzle, downward and forward. From the nostrils, which are situated high on the head, the anterior portion slopes at first gently then bends strongly down to the

FIG. 3.— Dugong's head, anterior view. *a*, lateral fold; *b*, lateral furrow; *c*, central area; *d*, median furrow; *e*, lower limiting fold; *f*, mandible; *g*, intermediate fold; *h*, incisor tooth; *i*, chin fold; *j*, palatal process.

mouth, to form the remarkable surface of the snout which is peculiarly modified on its lower portions. This area is broadly horseshoe-shaped, somewhat convex anteriorly, with the point directed a little obliquely forward and downward. It is from 22 to 24 cm. broad and 17 cm. high.

In the living animal the snout is soft and flexible and consists of a solid muscle mass traversed by fatty tissue, wherein the fiber bundles intersect in a complicated fashion as in the tongue. The skin of the snout is so very delicate and pliable that it may readily

be gathered into a very narrow fold between the fingers. The surface of the snout is differentiated into (1) a middle portion, (2) its ventral posterior fold, and (3) the two lateral folds. The middle area is of the shape of a broad horseshoe. On its lower part there is a sharp median furrow which becomes lost ventrally in the gums, and likewise disappears in the dorsal third. The anterior half of this furrow is much shallower than the posterior. The entire surface is striated with numerous wrinkles which can be seen to have definite courses. Anteriorly, curves predominate whose convexity is forward while posteriorly there start on each side of the median line numerous wrinkles, at first parallel with

FIG. 4.— Dugong's head, lateral view. *a*, lateral fold; *b*, lateral furrow; *c*, central area; *d*, mandible; *e*, incisor; *f*, chin fold; *g*, palatal process; *h*, chin; *i*, ear; *j*, fold at the flipper; *k*, furrow at the flipper; *l*, flipper.

one another, that radiate out towards the sides and, running forward, cross those first mentioned. On the folds thus produced stand thick short bristles. Dorsally the median surface of the snout passes into that of the general integument of the anterior dorsal region.

The demarcation of this middle area posteriorly is effected on both sides by a low broad fold which is crossed by the median furrow but begins at some distance from it and, becoming better defined laterally, passes downward and backward toward the corner of the mouth. Then on both sides it passes into the side fold of the middle area. Opposite the mandible, relatively opposite the gums, the lower fold becomes greatly enlarged though in the figure this feature does not appear since the flabby snout of the animal as it lay on its back, has sunken down. Nevertheless there is visible in this position an intermediate fold on both sides which fills the space between the corner of the mouth, the lower fold, and the mandibular process. The posterior limiting fold is likewise thickly set with the bristles previously mentioned. The middle fold, particularly toward the furrow, also shows these stiff, backwardly directed bristles.

The lateral folds are comparatively small and are separated from the middle area by a deep indentation. In the figure, these furrows gape apart on account of the depression of the snout. Numerous transverse wrinkles that intersect on the inner and outer sides, as well as an abundance of bristles along the borders are present on these lateral folds. They begin rather well up toward the dorsal part of the snout, and with a gentle lateral sweep, enclose the middle area and with a strong curve pass posteriorly toward the corners of the mouth. Here they merge with the posterior fold and at the same time the limiting furrow becomes very shallow. Beneath the snout and completely hidden by it when in the normal position, is the mandibular process covered by the gums. In the male this process bears on each side a short but stout incisor. The gum has a median anterior groove. Below the end of the mandible and the points of its projecting teeth is a strong firm palatal process that consists of solid fibrous tissue and reaches beyond the incisors. It is about twice as wide as thick (7 cm. to 4 cm.) and with its rounded anterior end bears a certain resemblance to the tip of a tongue. It is not retractile and is clearly visible between the jaws even when the latter are closed. From the fact that the furrows made in the sand by the dugong in grazing are of the same width as these palatal processes, it may be concluded that they play a part in the taking of food.

The shortened lower jaw is directed diagonally downward and extends backward with a breadth corresponding to that of the narrow mandibular cavity which is but 10 cm. deep. The anterior portion of the lower jaw is narrow and becomes rounded at the tip so that not only is it well set off from the neck but the angles of the mouth are also strongly drawn in. The transverse diameter of this chin-like projection is considerably greater than its length.

FIG. 5.— Dugong's head, ventral view. *a*, lateral fold; *b*, lateral furrow; *c*, central area; *d*, median furrow; *e*, palatal process; *f*, chin fold; *g*, chin.

The greatest length is in the plane of the mouth, for as is seen in profile, the outline of the chin starting from its origin at the neck, constantly recedes from the mouth till it bends down again to the tip of the jaw. The greatest transverse diameter is about in the middle between the corners of the mouth, along the line marking the origin of the chin from the neck, for the line defining the chin posteriorly is bent down on each side toward the corners of the mouth, like a pair of tongs. Along the margin of the mouth on

each side of the lower jaw is a low narrow ridge which is marked off by a slight furrow from the rest of the chin. This ridge as well as a broad adjacent strip of the chin is thickly set with short fine bristles. The remainder of the surface of the chin bears coarser and more scattered bristles each of which springs from a small dark pit, just as in the case of the fold at the edge of the mouth near the palatal process.

In reviewing the literature on this subject we will first consider the account given by Rüppel. Contrary to our observations, he states that the long median furrow of the snout is bifurcate ventrally so that its form is that of an inverted Y. By this bifurcation, this portion of the snout is divided into three parts, the two upper of which belong with the nose while the small lower triangular part forms the upper lips proper, directed toward the inner surface of the mouth. It is of course obvious that the long vertical furrow spoken of by Rüppel is identical with that described by us. The bifurcation which, as our description shows, has nothing particular to do with the median furrow, is the bow-shaped depression formed by the snout proper and the palatal process. The small three-cornered portion below is the palatal process, which of course has no connection whatever with the lips. Rapp speaks in only a general way of the Sirenian snout. He states that the upper jaw ends anteriorly in the form of a flat blunt disc richly provided with nerves, that perhaps functions as an organ of taste; and further, that in the case of the dugong particularly, the "lips" are very thick and they as well as the corners of the mouth toward the inner side of the cheeks bear thick stubby bristles. Krauss makes no mention of the median furrow of the snout but describes the side folds which Rüppel omits. Both authors give detailed accounts of the distribution of hair on the snout. Krauss, however, correctly describes the palatal process and the fold at the edge of the lower jaw. Brehm and Finsch make mention of the head in a few words as does also Owen who considered its peculiar form to be especially adapted for the taking of food. Turner gave an extended account of the head of an adult female dugong but a comparison of his figure with ours shows that the preservation of his specimen with dry salt must have been very poor for it is greatly shrunken and out of shape. In consequence, the descrip-

tion based on this specimen can be only partially followed. For the median furrow is brought into connection with the furrows between the middle area and the posterior limiting folds as if it were bifurcate. The side folds end in a point posteriorly and are not continued into the posterior fold, which instead comes from the lateral portions of the middle area (Figs. 3, 5). Turner describes the greatly shrunken palatal process in his specimen as "middle lip (mesial process)" notwithstanding that it has no genetic connection with the lips. The middle area, on account of its being cut by the median furrow, is misleadingly called "lateral lips," so that in considering the homologies of the parts mentioned, it is necessary to take into consideration the probable shrinkage that they have undergone.

Of particular interest, naturally, are the embryological conditions as pictured in Kükenthal's sketches of a freshly preserved fetus. These sketches are much more satisfactory than the figures of the fetus given by Turner. In all the embryos the deep median furrow of the middle area is apparent. In his fourth stage, Kükenthal was able to make out a shallowing of this furrow in the region of the lip. From the fact that this portion of the furrow was lacking in Turner's figure of the adult, Kükenthal concluded that a fusion had here taken place between two originally separate portions in such a way that the two lateral parts of the upper lip had become united medially. In further support of this view, he cited Rüppel's figure, which as we have shown above is to be otherwise interpreted and is thus unavailable as evidence on this point. In our specimen the median furrow extended to the gum, and, since Turner's figure is untrustworthy, it can hardly be held that the two portions of the middle area are united at the posterior part of the furrow. At the same time we do not wish to contest Kükenthal's conclusion that the snout of the dugong, which in the adult is rather simple, has become like that of the manatee through a division into a median area and two lateral areas and that thus the manatee's snout is phylogenetically the older. For with this conclusion we are in hearty sympathy. This third median portion is to be found at the upper end of the median furrow as indicated by its upper bifurcation in a fetus of 72 cm. (Kükenthal), and an almost horizontal bifurcation in a fetus of 162 cm. in length (Tur-

ner). At an early period the two lateral folds are formed and are marked off in the embryo by a lateral furrow which is wanting in the adult, or is apparent in certain places only (Kükenthal). The side folds, which at first converge dorsally in the embryo, later become parallel, and finally in the adult become divergent above. The growth in breadth of the middle area is correspondingly greater in its upper than in its lower portion. The two posterior limiting folds of the middle area appear to be formed later. They are figured by Kükenthal from an embryo 162 cm. long. In the embryo the surface of the snout is marked off into little spaces with a beautiful regularity and from the center of each knob-like space rises a hair. The form of the palatal process and of the lower jaw in the embryo is not greatly different from that of the adult.

A short distance above the snout are the blowholes. These are two almost circular openings, close together and directed obliquely upward and forward on the muzzle. Owen characterizes their high dorsal position on the curve of the intermaxillary as one that is very advantageous for breathing. In our figures the nostrils are open, as usual in dead specimens. When the nostrils are closed, the muzzle is arched forward and slightly rounded. In our specimen we found nothing that might be called a valve-like structure, such as Rüppel and Turner mention, but this subject we have treated at length in our previous paper as regards both the dugong and the manatee (*Amer. Nat.*, vol. 40, pp. 49–72).

The eyes are situated on the side of the head, 18 cm. behind the tip of the nose in specimens of average size, and are about equidistant from the end of the snout and the corners of the mouth. They are visible through a narrow spindle-shaped opening that slants obliquely upward, and is 12 mm. long (Owen also). The eyelids are thick and tumid, and only feebly movable up and down; they are provided with a contractile muscle, the musculus orbicularis oculi. At the anterior corner the nictitating membrane is clearly visible (*cf.* also Rapp and Owen). There is no trace of eyelashes although Brehm speaks of them regardless of Rüppel's correct assertion that they do not exist. The bulbi are small and nearly spherical, though not egg-shaped as Brehm states. The iris and choroid layer are black-pigmented so that the whole eye appears dark.

In the region where the head passes into the neck, there is on each side of the former, at the end of a transverse series of neck furrows, the small ear opening. This is in a scarcely noticeable depression of the skin about 3 mm. in diameter, at about the same level with the eye and some 15 cm. behind it. There is no external ear and Turner found none in the embryos.

The external form of the two pectoral appendages, which arise not far from the head toward the ventral side of the body and project laterally, has been rather exhaustively treated in a work on their osteology by Freund. It remains to say, however, that the flippers are usually directed backward along the sides of the body, so that a thick fold arises above the furrow at the insertion. The upper surface is darker than the lower. The absence of hair on the flippers has already been mentioned. In the adult animal, the extreme length of the flipper is not over 32 cm., and the greatest breadth is 20 cm. or a trifle more.

The mammæ are short, hard, cone-shaped structures as thick as one's thumb. They are situated, one on each side, in the axillary region, behind the furrow of the flipper, as Owen and Rüppel also state, and are seen well from the ventral side. According to Owen, their bases in the case of a female specimen were about the size of a shilling, and they rose about one half an inch above the surrounding surface. Turner found no trace of mammæ in an embryo 162 cm. long.

As to the rest of the body there is but little to be said on account of the few peculiar characters it possesses. In the middle of the belly is the navel and 40 cm. behind it is the preputial opening or the vaginal furrow as the case may be. The latter is a slight cleft about 10 cm. long (*cf.* Klunzinger also) and is hardly to be differentiated from the anus. It lies slightly nearer the middle of the tail — 90 cm. (100 according to Klunzinger) — than the penis which is from 132 to 156 cm. distant from the navel. On these points Bischoff has published some observations. The anal opening and the vagina are closer together than are the penis and the anus. In animals that have been dead in the nets for some time and in which decomposition has begun, the penis is usually prolapsing. It is covered by an unpigmented skin and ends in a conical point with two large lateral lips.

The caudal portion of the body consists of a horizontally flattened fin, with a very slight indentation at the posterior margin. Its breadth is from 77 to 82 cm., and on this point Raffles and Owen also agree. There is no indentation in the shape of a half moon such as Rapp, Rüppel, and Brehm mention, but the posterior margin is feather-edged and often is considerably torn. According to Owen the tail is relatively larger than in the whales, and this he explains as due to the frequent necessity for coming very quickly to the surface for breath while feeding.

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REPRODUCTION OF *METRIDIUM MARGINATUM* BY FRAGMENTAL FISSION

M. L. HAMMATT

DURING the autumn of 1897, a specimen of *Metridium marginatum*, about one half an inch in diameter at the base, was kept by the writer for some weeks in a glass jar in an open north window. Its favorite resting place was near the edge of the sea water, where it could be plainly seen both from above and through the side of the glass. One morning it was noticed that its tentacles were withdrawn, that it had evidently moved toward one side, and that whereas the night before its basal outline had been quite regular, it now showed a slight inward curve, opposite to which, at a short distance from it, was a fragment which had evidently been divided off during the night. The separation between the two was not quite complete, as a transparent thread passed from one end of the fragment to the parent form, disappearing, however, soon after. The distance between the two was gradually increased and the fragment was seen to possess life, because it changed shape from time to time.

This fragment was carefully watched for a few days and was seen to curl together gradually until its extremities met, but the opportunity for following its further development was wanting.

Later on it was discovered that this reproduction by fragmental fission in Metridium was mentioned by Verrill in an article entitled "Our Common Sea Anemone" in the second volume of the *American Naturalist*, also that similar reproduction in *Anthea cereus* was noted by Gosse, in *Sea Anemones and Corals*, 1860 (page xxi of the introduction and page 169), and in Tenby, where he states, on page 373: "If the body be torn away and only a portion of the base remain, from this fragment a new offspring will sometimes

rise up to occupy the place of its parent." Dicquemare and Dalyell also observed the same mode of division in sea anemones.[1]

When the observation of the writer as above recorded was mentioned to Professor A. Hyatt, he remarked that reproduction by fragmental fission in *Metridium marginatum* had not, to his knowledge, been thoroughly studied and figured, and suggested the advisability of pursuing the investigation further with a view to publication, adding that a series of drawings illustrative of the process observed would be of value as an aid in the teaching of asexual reproduction. In accordance with this suggestion and in the hope of ascertaining whether forms thus produced developed later into whole organisms, more small specimens of the same genus were collected in June, 1898, in the same tidepool from which the former Metridium mentioned had been taken. This tidepool was a small one and in it, especially along the edge, under the overhanging seaweed, the Metridia were numerous. Fragments were sought for and readily found in abundance not far from the mature forms. These were in various stages of the process of curling together and obviously had been produced by fission similar to that already observed within doors. One of these fragments which was larger than the others had partly curled together and on the next day the ends had come in contact and two tiny prominences, apparently the beginnings of tentacles, had appeared.

On examination of this same tidepool at various times since then, like fragments have always been found. They showed generally neither tentacles nor mouth, and their irregular, elongate shape, not having taken on the radiate form, also their brownish color,

[1] Since writing the above paper, my attention has been called to A. Andres' publication "Intorno alla scissiparita delle attinie," (*Mitteil. Zool. Sta. Neapel*, vol. 3, pp. 123–148). My observations were made without any previous knowledge of those of Professor Andres or of any other naturalist. They were also made on a different species. Moreover, my figures show three points not illustrated by Professor Andres, or to my knowledge, by any other authority: first, oral views of successive stages of development of the young produced by fragmental fission (laceration) showing the *completion* of the curling process by which the young assumes the parent form; second, serial, transverse sections of parent and young in process of fragmental fission showing the infolding of the body wall preceding the separation of the two; third, diagrams illustrative of the process of such fission.

distinguished them from the transparent young developed from the ovum.[1]

The Trembley experiments previously performed on the hydra suggested the pursuance of the same method with *Metridium marginatum*, hence on Wednesday, June 15, 1898, at 2 P. M., the fragment figured at Plate 1, Fig. 1, was produced by artificial fission from the base of a specimen one fourth of an inch in diameter. The Metridium threw out one acontium near the mouth and several where it was cut, and drew in its tentacles entirely. When cut off the fragment fell to the bottom of the glass as if it were without life, and had to be turned over with a needle so as to rest on its base. This fragment was kept under careful observation every day for a period of three weeks and, from studies taken from time to time, the accompanying drawings were made.

The lines crossing Fig. 1 (Pl. 1) nearly at right angles to its length represent portions of the radiating mesenteries of the parent form as seen through the body.

At 2.15 P. M. of the same day the Metridium had extended its tentacles, and in the fragment, as seen in Fig. 2 (Pl. 1), the extremities were approaching each other.

Fig. 3 (Pl. 1), drawn at 4.30 P. M. of the same day, shows a nearer approach of the ends and a difference in size, whether due to growth or to the re-assertion of the power of expansion possessed by the normal animal.

In Fig. 4 (Pl. 1), drawn Tuesday, June 21, at 2 P. M., is seen a greater elevation of the column and a more spreading base, although the ends have not yet joined.

In Fig. 5 (Pl. 1) drawn on Wednesday, June 22d, at 10 A. M., the extremities of the fragment have come together, thus producing, approximately, the normal radiate structure of the sea anemone, leaving, however, a slight inward curvature at the point of junc-

[1] Since the above observations were recorded, a number of these fragments, already beginning to curl together, have been carefully collected and placed in a jar where the successive stages leading to their maturity have been followed. They have been found to develop in essentially the same way as did the artificially produced fragment described farther on. The ends of one unusually long fragment curled in opposite directions. Could this latter suggest the origin of many of the double-mouthed Metridia found?

ture. The base here is a trifle more extended and the column, as shown in Fig. 6 (the side view of Fig. 5), is much more elevated.

On Thursday, June 23d, at 11.30 A. M., Fig. 7 (Pl. 1) was drawn. Here the young form shows translucent prominences afterwards recognized as the beginnings of tentacles, the one at the line of juncture being less developed than the others. This line of juncture is still visible up as far as the tentacles and makes a slight irregularity at the base. The mouth could be discerned but faintly at this time.

Fig. 8 (Pl. 1), the side view of Fig. 7, shows the tentacles more plainly.

Fig. 9 (Pl. 1), represents the young form as it looked on Saturday, June 25th, at 3 P. M. It shows a further development of tentacles and mouth and an increase in size.

In Fig. 10 (Pl. 1), the side view of Fig. 9, the line of juncture is seen to have disappeared throughout the upper third of the column. In Fig. 11 (Pl. 1), drawn on Saturday, July 2d, the hour not noted, this line is still fainter and shorter and a further increase in the size of the animal is indicated. At this time the young Metridium was very active, crawling along the glass at the edge of the water. Ten tentacles were visible, unequal in size. Lack of symmetry is especially noticeable here and in the following figure. This same lack of symmetry holds in all observed forms which were produced by fragmental fission. Whether these forms ultimately become symmetrical is not known to the writer.

Fig. 12 (Pl. 1), was drawn on Wednesday, July 6th, just before the young Metridium was put into formalin. This shows a further growth and a development of two more tentacles, making twelve tentacles in all.

Thus in the three weeks, from Wednesday, June 15th, to Wednesday, July 6th, a fragment from the base of a small *Metridium marginatum* curled together until its extremities met, developed a spreading base, a column, twelve tentacles, and a mouth, and must therefore have performed the nutritive functions, as evidenced also by the increase in the size of the animal. This experiment of artificial fission was repeated several times on other Metridia with similar results.

During the examination of microtome sections of small Metridia

at about this time, for the purpose of studying the microscopic structure of the animal, one Metridium revealed the serial sections figured in Plate 2. These figures are slightly diagrammatic, as intended to illustrate merely the point under consideration. From a study of these sections, if the above observation of reproduction by artificial fragmental fission be borne in mind, the inference may be drawn, that at the time of killing, the Metridium from which the sections were taken was preparing to reproduce asexually by cutting off a fragment.

In Fig. 1 (Pl. 2), either the cutting was not parallel to the oral disc, or the column was unevenly distended vertically, as the tentacles are seen on but one side, that opposite to where fission takes place. This is also noticed in sections shown in Figs. 2 and 3 (Pl. 2). The same fact was noted in regard to similarly placed serial sections of other Metridia examined, which were reproducing in the same way.

In Fig. 1 (Pl. 2), the uppermost in which fission is visible, the separation between parent and fragment is seen to be complete. Portions of the old mesenteries reaching from the outer to the inner body wall are visible in this section in the young.

In Fig. 2 (Pl. 2), the fragment cut off is longer than in section 1, but the separation between the two is not quite complete.

In Fig. 3 (Pl. 2), the infolding of the body wall which makes the division between parent and fragment is not continuous as in sections 1 and 2. The break is seen toward that extremity of the body where the tentacles are visible. This break in the continuity of the fold in the section may be due to a slight irregularity in the folding. No separation between parent and fragment, such as was seen in sections 1 and 2, has as yet taken place. The fragment here cuts off a greater proportion of the parent body than in the section before considered. It is also wider and shows longer mesenteries. Bilateral symmetry is here evident in the parent after the infolding of the body wall which is to cut off the fragment. This same fact is noticed in sections of other Metridia in which like fission is taking place.

In Fig. 4 (Pl. 2), the dividing fold is seen pushing inward from either side, evidently about to cut off here a still larger proportion of the parent than in Fig. 3. It will be noticed here, where the

ends of these folds are as yet far from meeting that, previous to fission, there has been an increase in size on the side where this is to take place. This seems to be in accordance with the general rule that extra growth usually precedes fission.

Fig. 5 (Pl. 2), shows the folding of the body wall extending inward but little from either end. One of these folds shows new mesenteries growing from the side which is to form the inner surface of the body wall of the parent. In this section the fact is still more apparent that, before fission occurs, the parent form lacks bilateral symmetry and that the division takes place on the larger side.

The same is seen in Fig. 6 (Pl. 2), which shows only the beginnings of the inward foldings of the body wall, after the completion of which the parent form is to be approximately symmetrical.

In the other sections between that shown in Fig. 6 and the base or pedal disk, the same conditions hold with regard to lack of symmetry as related to the side upon which fission takes place. The body wall shows no inward folding here, but judging from the artificial and natural fission observed, the folding would eventually have reached the base.

In all the sections shown, the line *a. b.* passing between the two pairs of directive mesenteries, *d. m.*, represents the plane of symmetry of the parent animal. The fragment is seen to be divided off on one side only of this plane.

The study of serial sections of other Metridia showed the complete and the partial infolding of the body wall essentially like the above, and evidently preceding fragmental fission.

In consideration of the facts as observed and stated above, the following conclusions are reached by the writer as to asexual reproduction in *Metridium marginatum* by fragmental fission. This occurs in nature as observed in the jar within doors and as seen in the tidepools; also as indicated by the sections. It occurs frequently, as shown also by observations on tidepools.

From the study of sections it is inferred, that the body becomes bilaterally asymmetrical before fragmental fission takes place, this occurring always, as far as observed, on the larger side and that the fragment thus cut off includes body wall (formed on the side next the parent by infolding of the parent body wall), and

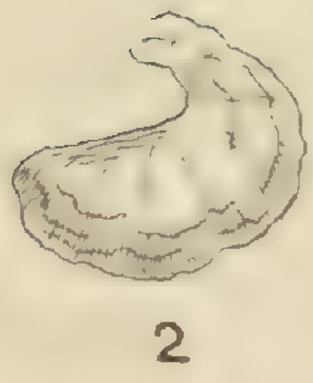
parts of directive and other mesenteries on one side only of the plane of symmetry of the parent animal. The sections show also that the infolding of the body wall proceeds gradually, and simultaneously downward and inward from the top and upper part of the sides, and that separation of the fragment from the parent commences at the top, as indicated by diagrams (Figs. 7 and 8, Pl. 2).

This infolding of the body wall here, to separate the fragment from the parent form, seems to be essentially the same process as the constriction which divides the Hydra bud from its parent, but here the basal attachment modifies the process by preventing the infolding on that side and by keeping the fragment close to the parent until separation is complete. Whereas in Hydra, a thread tied between parent and bud would represent the method of division, in Metridium the thread may be imagined as held down at either side of the pedal disk and gradually tightened along the line which is to separate parent from fragment, thus producing an infolding proceeding downward from the top and inward from the upper part of the sides.

Observations of the young naturally and artificially produced by fragmental fission show that the fragment cut off curls together until its extremities meet, making parts of mesenteries before nearly parallel now radial in arrangement, thus attaining to the sea anemone structure with the least possible expenditure of energy. From artificial fragmental fission principally, it is seen that the base or pedal disk spreads for attachment, the column becomes elevated, the line of juncture tends to disappear, mouth and tentacles develop, and growth in volume apparently takes place; that the young thus produced, possesses the power of locomotion and that it is, in fact, a whole organism, and, except for the fact that it has not yet attained symmetry, is essentially, in outward appearance at least, a smaller reproduction of its parent.

Obligations are due to Dr. A. G. Mayer for reading this paper, to Mrs. J. M. Arms Sheldon for valuable suggestions, and to Professor G. H. Parker for the determination of specimens; also to the artist, Mrs. A. M. Dodge, for faithful delineation of specimens and sections.

1



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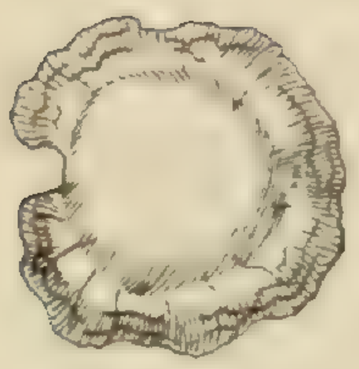

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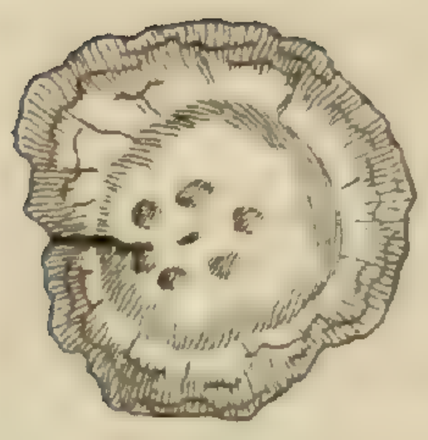

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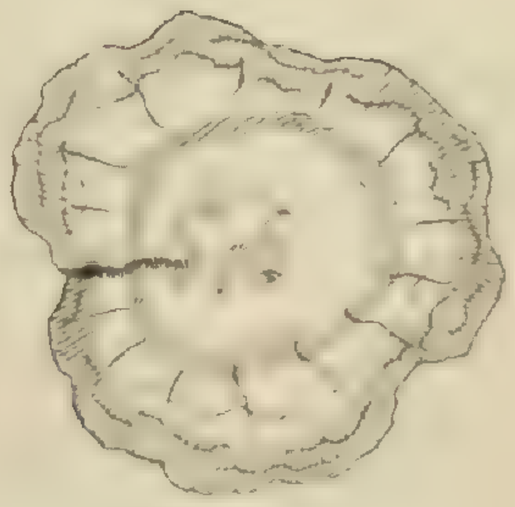

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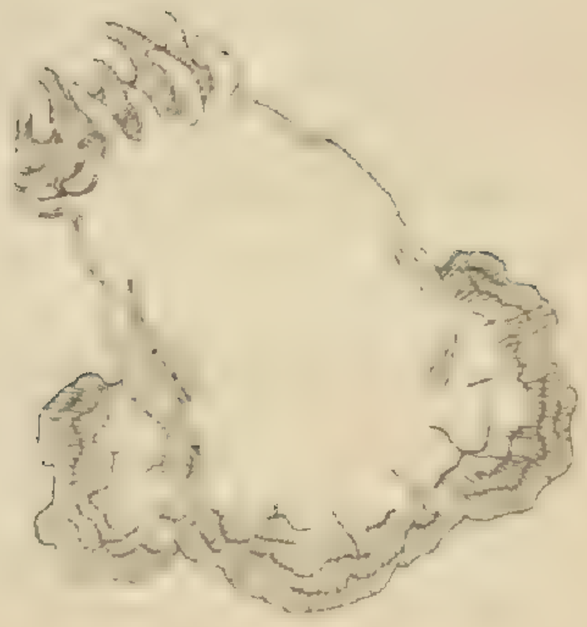

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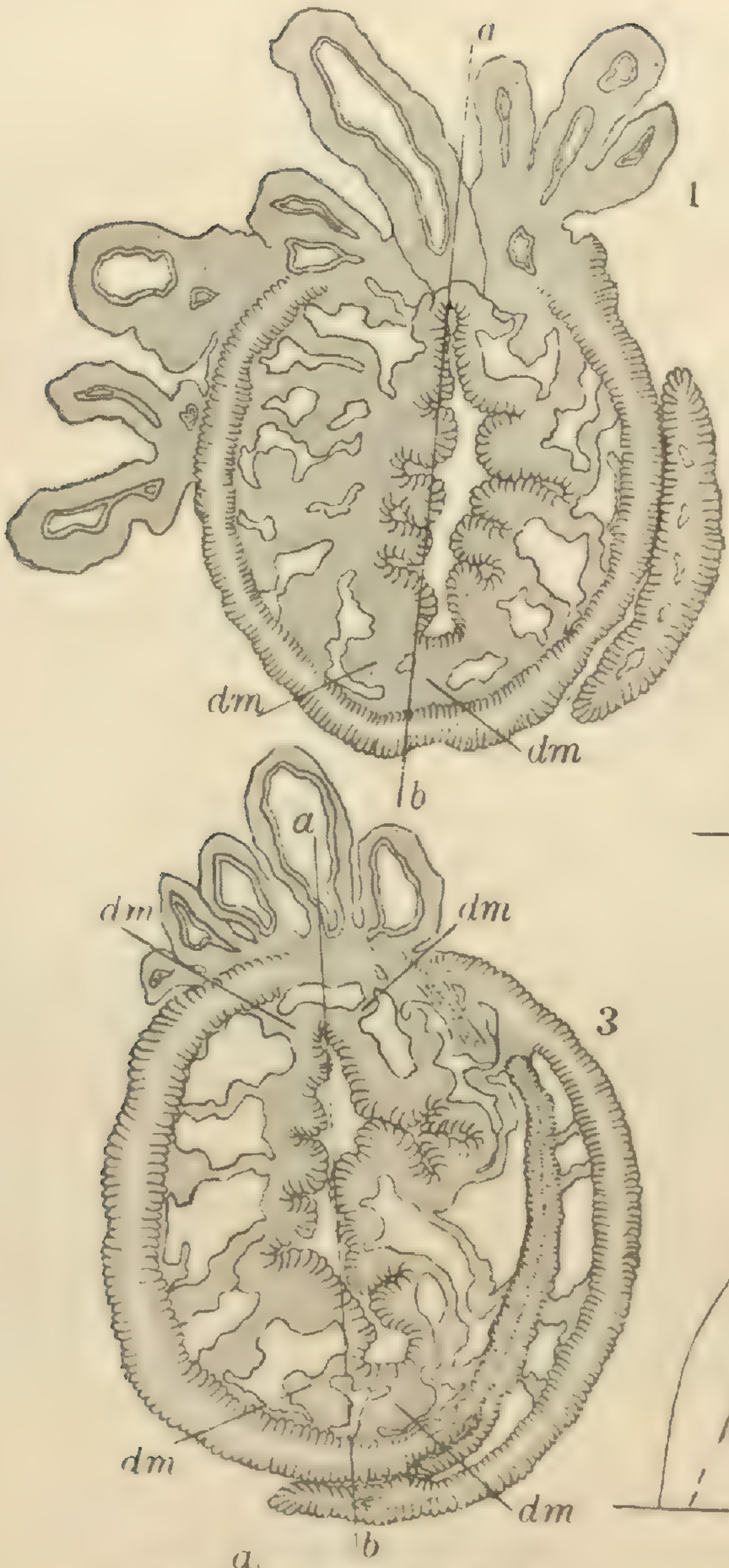
PLATE 1.



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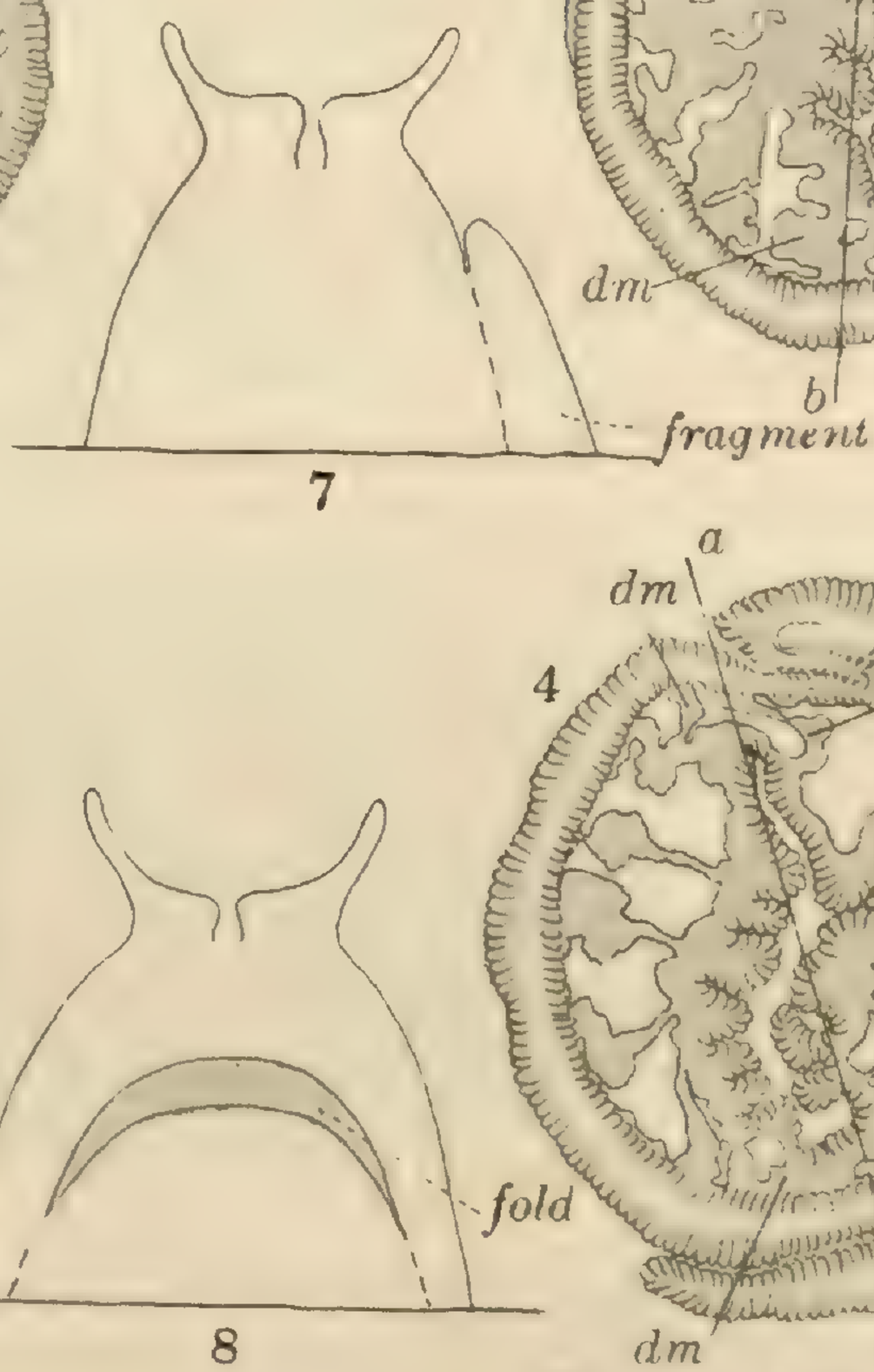

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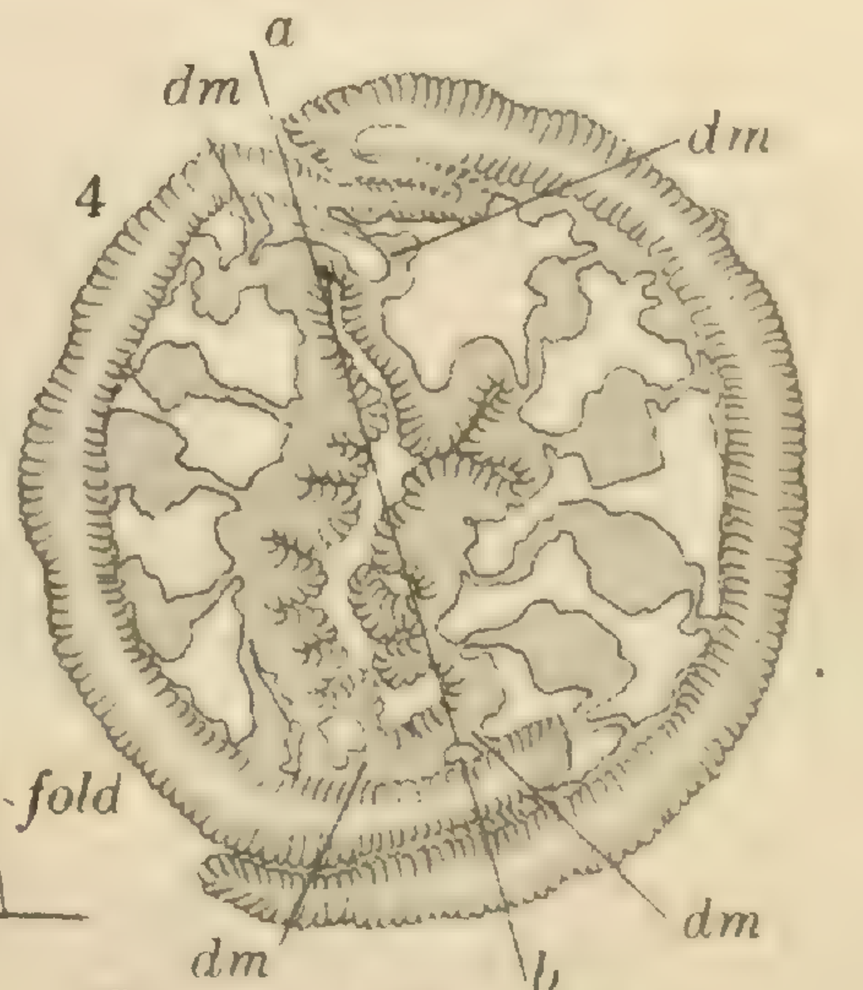

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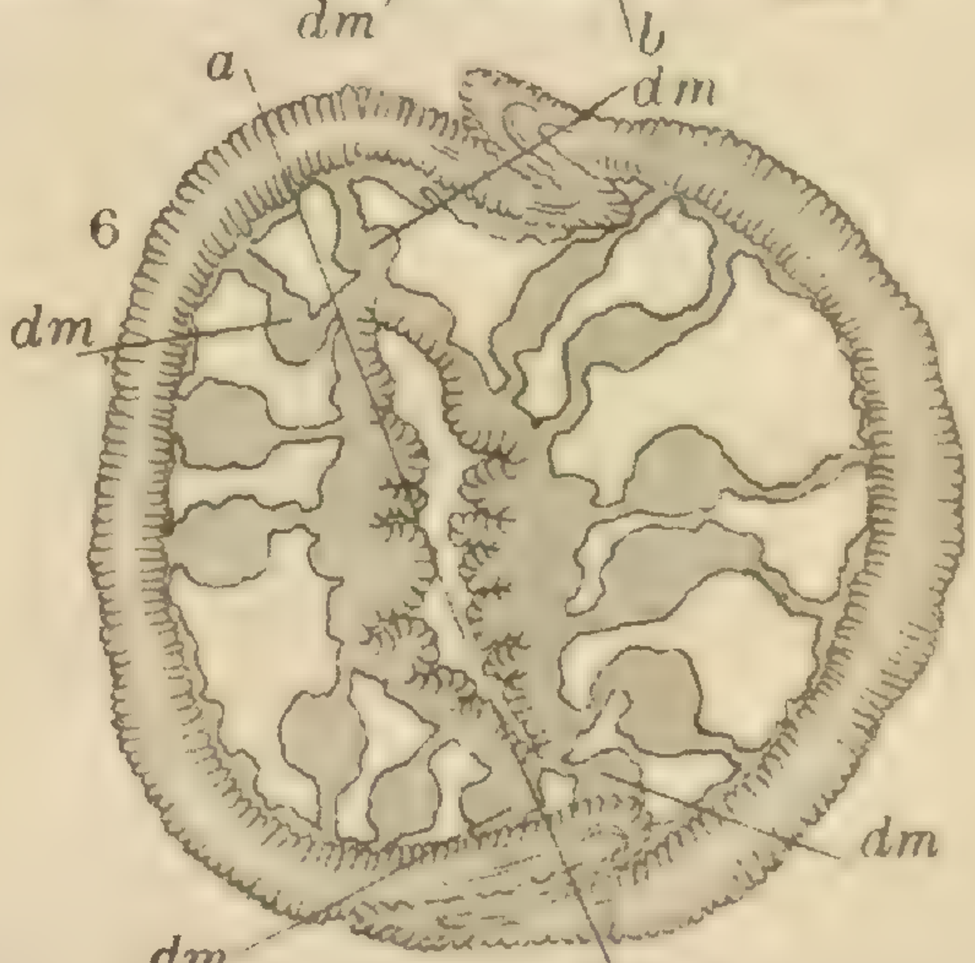

6

PLATE 2.

NOTES AND LITERATURE

ZOÖLOGY

Plankton of Northern Seas.[1]— The earlier parts of this series of monographs (see this journal, vol. 39, p. 341) have been supplemented by two additional sections containing six more papers dealing respectively with the pelagic annelids, chætognaths, Rotatoria, Acantharia, Radiolaria (Acanthometrida), diatoms, and a portion of the pelagic eggs and larvæ of the fish of northern seas, that is of water north of 50° N.

The papers on the pelagic annelids and the chætognaths are necessarily brief, the former including only nine, and the latter but seven species. Dr. Strodtmann follows Krumbach in making use of the grasping teeth of Sagitta as diagnostic characters for specific distinctions. The pelagic rotifers are somewhat more fully treated by Dr. Lauterborn. As yet the marine rotifers are very incompletely known, except in the Baltic and North Seas. Only sixteen marine and brackish water forms have as yet been found in northern waters. About forty additional species of fresh-water rotifers are known to enter the seas but they are adventitous and do not become acclimated to the marine habitat, except in a few cases, in which marine varieties of fresh-water species are known, as for example in *Anuræa aculeata* var. *platei*, and *A. cochlearis* var. *recurvispina*. The marine species are all coastal or brackish-water forms, none being known as yet from the high seas.

Dr. Popofsky's monograph of the Acantharia (sublegion Acanthometra) will be especially welcome as it embodies the revision which he has recently completed of this group, the first to be made since the publication of Haeckel's monograph of the Radiolaria. The author

[1] *Nordisches Plankton*. Herausgegaben von Prof. Dr. K. Brandt und Dr. C. Apstein. *Dritte Lieferung*. M. 10. X. Anneliden, J. Reibisch, 10 pp., 15 figs.; Die Chætognathen, S. Strodtmann, 8 pp., 11 figs.; Nordische Plankton, Rotatorien, R. Lauterborn, 25 pp., 17 figs. XVI. Die nordischen Acantharien. I. Teil and Nachtrag, A. Popofsky, 27 pp., 20 figs. XIX. Diatomeen, H. H. Gran, 146 pp., 178 figs. *Vierte Lieferung*. M. 10. III. Eier und Larven von Fischen, I. Teil, E. Ehrenbaum. Kiel und Leipzig, 1905, large 8vo. 216 pp., 82 figs.

takes a justly conservative ground in the matter of species in this group and is much inclined to question the reported occurrence of certain forms in northern waters. He notes the solubility of the skeletal structures (calcium-aluminium silicate or hydrate) in acids, alkalis, sea water, or distilled water, and rejects species founded on "skeletlos" specimens.

Professor Dr. Gran's treatment of the diatoms of the plankton will be most welcome to all planktologists, for no comprehensive monograph of these organisms has appeared since that of Castracane in the *Challenger Reports*, and this unfortunately is far from complete. The more recent investigations, especially of Schütt and Cleve, have added greatly to our knowledge of the pelagic genera, but this revival of interest has been attended by considerable duplication and confusion in synonymy. The author's wide experience with these organisms makes his critical monograph most timely. The monograph includes nearly 300 species, most of which are figured. Excellent keys to both genera and species are found throughout the paper. It is perhaps desirable that the chromatophores should be more completely utilized in the description of species and that their position in the cell should be interpreted with reference to the vertical distribution in the sea and consequent exposure to light.

The first section of Dr. Ehrenbaum's account of the eggs and larvæ of the northern fishes found in the plankton includes nearly ninety species from about thirty families ranging from the Labridæ to the Pleuronectidæ. Although it does not include some families of greatest economic importance in northern seas, as for example the Clupeidæ and Gadidæ, this first part nevertheless contains much of interest along economic and fish-cultural lines. The young of nearly all, and the eggs and larvæ of many fishes are taken in the plankton. The pelagic habit is, however, of little systematic significance since the young of species of the same genus are in some instances pelagic, in others benthic in distribution. The author notes the significance of dimensions and pigmentation as diagnostic characters of the young and urges the importance of the examination of living material. Preserved eggs and larvæ, even in the best condition, are not readily determined. The size of the eggs, and of the characteristic oil globules, and the number of fin-rays, and to a less extent the number of vertebræ, are subject to considerable variation. It is noteworthy that the range of this variation increases with the area of distribution of the species, and with the length of the breeding period under observation.

The author's account is abundantly illustrated with over three

hundred figures many of which are original. The excellent work of the Helgoland Station is evident on many of the pages of this comprehensive report.

The authoritative character of the papers in this series insures for them a wide range of usefulness and a permanent value to all naturalists who are concerned with the pelagic life of the sea.

C. A. K.

Notes on Pennsylvania Fishes. *Notropis cayuga Meek.*— Early in August of 1904 I secured a single example of this minnow in the Allegheny River, above Port Allegany, in McKean County. This is, I believe, the first record within our limits. Other fishes noted from this locality were *Lampetra wilderi*, *Salvelinus fontinalis*, *Campostoma anomalum*, *Semotilus atromaculatus*, *Leuciscus elongatus*, *Rhinichthys atronasus*, *Catostomus commersonnii*, *C. nigricans*, *Erimyzon sucetta oblongus*, *Schilbeodes insignis*, *Esox vermiculatus*, *Ambloplites rupestris*, *Eupomotis gibbosus*, *Micropterus dolomieu*, *Boleosoma nigrum*, and *Uranidea gracilis*. In the summer of 1899 I noted *Polyodon spathula*, *Campostoma anomalum*, *Leuciscus elongatus*, *Notropis hudsonius*, *N. whipplei*, *N. cornutus*, *Rhinichthys atronasus*, *Stizostedion vitreum*, and *Boleosoma nigrum* from streams near Cole Grove and other places along the Allegheny.

In the Susquehanna tributaries in Cameron County during October of 1905, I noted *Lampetra wilderi* (apparently this species though I did not see it myself), *Semotilus atromaculatus*, *Leuciscus vandoisulus*, *Brama crysoleucas*, *Notropis cornutus*, *Rhinichthys cataractæ*, *R. atronasus*, *Exoglossum maxillingua*, *Catostomus commersonnii*, *C. nigricans*, *Schilbeodes insignis*, and *Boleosoma nigrum olmstedi*. All these species occur near Emporium. *Notropis amœnus* occurs near Paradise, in Lancaster County, where I have received it from Mr. J. S. Witmer.

Mesogonistius chætodon (Baird).— The only place where I have found this sunfish in Pennsylvania has been in the basin of Mill Creek in Bucks County, near Bristol. It seems to occur sparingly, and most all of my examples were secured in the colder months. I have not found any previous definite records for Pennsylvania.

Boleichthys fusiformis (Girard).— I have only found this in the same locality as the former in our State. The first example was secured July 23, 1905, and on December 24 of the same year I found it very abundant. Though known from the lower tributaries of the Delaware in New Jersey, this fish has never before to my knowl-

edge been taken in Pennsylvania. The conditions where I secured my examples were similar to those found about Crosswicks Creek near Trenton, where the species is more or less abundant, though perhaps not so characteristic as in the lower lands. On the latter date *Anguilla chrisypa*, *Notropis chalybæus*, *Brama crysoleucas*, *Erimyzon sucetta oblongus*, *Esox americanus*, *Umbra pygmæa*, *Shilbeodes gyrinus*, *Aphredoderus sayanus*, *Enneacanthus gloriosus*, the above mentioned Mesogonistius, *Eupomotis gibbosus*, the above Boleichthys, *Aromochelys odoratus*, larval Desmognathus, Cambarus, larval dragon-flies, and hosts of Crustacea and shrimp, Gammarus, were also taken.

Enneacanthus obesus, contrary to Cope's statement that it is rare, is fairly abundant in southeastern Pennsylvania, though apparently local. I have received many living examples from the "Neck" in the lower part of Philadelphia.

HENRY W. FOWLER

Note on Muhlenberg's Turtle.—While spending a few days in late April with Mr. T. D. Keim in the region of Cedar Swamp Creek, Cape May Co., N. J., we observed a number of turtles about the fresh-water pools at the edge of the salt-marsh near Palermo. A single example of *Clemmys muhlenbergi* was found in this locality, a fact of some interest as the species does not seem to have been noted from southern New Jersey before. As an upland animal its distribution may be explained to some extent by the appearance of *Calopeltis obsoletus* at Stone Harbor, recorded by Mr. Witmer Stone in this journal for 1906, p. 166. In fact, most of the narrow strip on the Cape May County seacoast shows traces of upland life, the intervening cedar-stained streams presenting usually peculiar features. *Kinosternon pennsylvanicum*, *Chrysemys picta*, and *Clemmys guttatus* were abundant as noted in sequence. *Chelydra serpentina* and *Terrapene carolina* were also found, together with *Natrix sipedon*, *Thamnophis sauritus*, *Rana pipiens*, *Hyla pickeringii*, *Acris gryllus crepitans*, and *Bufo lentiginosus*.

HENRY W. FOWLER

ANTHROPOLOGY

The Bontoc Igorot[1] is a well written and abundantly illustrated contribution to the ethnology of this interesting branch of the Malay people. The work is the result of the author's eight and a half months' stay among the Bontoc and other divisions of the tribe. It embraces a geographical and a historical sketch of the Igorots, notes on their physical characters and pathology, and descriptions of their social life and organization, economic life, political life, war and head-hunting, æsthetic life, religion, mental life, and language.

The word Igorot means "mountain people." The several branches of the tribe occupy northern Luzon, north of the 16th degree of north latitude. They are estimated collectively at from 150,000 to 225,000. The principal dialectic groups are Tinguian, Kalinga, Bunayan, Isanay, Alamit, Silipan, Ayangan, Ipukao, and Gadan. The Bontoc Igorots are so called after their principal village and the province.

The Bontoc Igorot (represented at the Louisiana Purchase Exhibition in 1904) is "a clean-limbed, well-built, dark brown man of medium stature." The men average 1.60 m. (5 ft., $4\frac{1}{8}$ in.) in height and are prevalently mesocephalic and mesorhynic. They are never corpulent and seldom thickset, their bodies being generally well formed and symmetric. The hair is black and straight, and the eyes brown. The women average 1.46 m. (4 ft., $9\frac{3}{8}$ in.) in height and more among them show a tendency to brachycephaly. The detailed description reads much like that of the American Indian and it is remarkable how many of those pictured in the book approach types often seen among the Indians.

The people are very primitive and wear but little clothing. Their principal occupation is agriculture. They are industrious, the social life is lowly, marriages are monogamous. "The social group is decidedly democratic; there are no slaves." There are but a few vices. The religion is animism and spirit belief, with the idea of one god. In disposition the people are kind and not servile. They are trustworthy. They possess a good sense of humor. The children are bright and learn quickly. The author has the best hopes for the future of the people.

[1]Jenks, A. E. *The Bontoc Igorot.* Ethnological Survey Publications. Vol. I, Manila, 1905.

The work is full of interesting details. The illustrations are mostly reproductions of very good photographs. Possibly it would have been better if the 154 plates had been bound separately; it would make the book easier to handle.

The creditable volume of Mr. Jenks leaves the earnest desire that it may be followed by a thorough physical and physiological study of the same people.

A. H.

Notes.— *Origin of the Slavs.* A comprehensive article (Zaborowski, "Origine des Slaves," *Bull. et Mém. Soc. d' Anthrop., Paris*, ser. 5, vol. 5, no. 6, Dec., 1904, pp. 671 720), in which the well known author sums up his investigations. The original country of the Greeks, Umbro-Latins, Gauls, and Germanic peoples was treated of previously. All these groups do not appear in history at the moment of their separation from their proto-Aryan territory; but they can be followed nearly to the limits of this region.

The Greeks were the first to gain their historic possessions. Their migration is lost in the obscurity of time. They occupied, in all probability, a part of the territory northeast of the Adriatic, living in those neolithic villages characterized by abundance and great variety of artistic pottery, such as that of Butmir, near Serajewo, Bosnia.

The Umbro-Latins, coming from the northeast, can be well studied in the remains of their habitations known as *terramares*, in the provinces of Emilia and Marches, northeastern Italy. They were still at that time in close relation with the proto-Aryan people of the Danube.

The home of the proto-Gauls was adjacent to and partly blended with the proto-Aryan region. It was located, as is known with certainty, along the upper Rhine and upper Danube, and extended thence to more or less determined limits northward and eastward.

The original proto-German country the author places, on the basis of archeologic and even historic data, in the lands west of the Baltic, where these people lived since at least the neolithic period.

To determine the exact origin of the Slavs is more difficult. The earliest historic accounts show them already spread over vast spaces and over regions very distant from one other. The hypotheses that they came as they were from Asia, or were identical with the Saramates, are untenable. The most creditable sources all refer their origin to the Danube (especially lower Danube region). Their language, belonging to the *satem* group, could not have originated except

in the zone east of the proto-Aryan territory. The linguistic ancestors of the Slavs spread over the Danube basin when the Umbro-Latins and Greeks on one part and the Gauls on the other were drawing away from it, or had abandoned it. They came after these peoples.

It is now known that the Illyrians, Pannonians, Dacians, Moesians, and Gétes were all Slavs. Originally, the Illyrians appear to have been one of the proto-Aryan peoples, but this element among them was eventually displaced by that which is characteristic of the Slavs. The introduction of this new element is believed to have been due to the Paphlagonians, and to have taken place after the Trojan war, or during the twelfth century B. C. The Paphlagonians were the neighbors of the Cappadocians in Asia Minor, and related to the proto-Armenians and Medes. They aided Troy and after its fall are supposed to have passed to Thrace, adopted the language of the Thracians and Illyrians, and mixed with these. They were people of dark complexion, with a rather short nose and brachycephalic; and they cremated their dead. The first Slav political unit appears as the Venedes, or Venetes. This people penetrated to the northeastern regions of what is now Italy. Their type and in a few localities even the Slavonic language are still found in these regions. From this locality they spread, still many centuries before Christ, northward and northeastward, to Bohemia, to beyond the Carpathians, Vistula, Dniester, and up to the Baltic. They founded Vindobona (Vienna) and their name persists with modifications in a number of localities (and as a name of a Slavonic people, the Wends), to this day. Wherever they went up to the time of christianization (8th to 12th century of our era) they practised incineration of their dead, and theirs is the industry known in archeology as that of Hallstadt.

For many interesting details the reader must be referred to the original.

A. H.

BOTANY

Plants and Light.[1]—A paper of Professor Julius Wiesner, dealing with the quantitative and qualitative light-relations of plants, is of particular interest to American botanists, since it records the results of observations made in the United States.

Some twelve years ago, Professor Wiesner, who fills the chair of plant physiology at the University of Vienna, led by his studies on the relation of light-intensity and heliotropism on the one hand, and that of light-intensity and carbon-assimilation on the other, inaugurated a series of observations on the effect of light-intensity on the form of plants. The discovery that the process by which the plant assumes its form depends on the influence of rays different from those which take part in photosynthesis, opened an entirely new field of investigation, and rendered the measurement of the highly refractive rays a necessity.

Various methods answering the latter purpose existed, the principal one being that of Bunsen and Roscoe, in which a standard photographic paper is exposed to light; the tone obtained is then compared with a standard black. In the course of the investigations various improvements in the method, such as a substitution of a color-scale for the standard black, suggested themselves. Detailed accounts of method and improvements are scattered through Professor Wiesner's numerous papers, but may be found more especially in his earlier publications.[2]

These measurements of light-intensity are based on the law of Bun-

[1] Wiesner, J. "Untersuchungen über den Lichtgenuss der Pflanzen im Yellowstone Gebiete und in anderen Gegenden Nordamerikas. Photometrische Untersuchungen auf pflanzenphysiologischem Gebiete. (V. Abhandlung.)" *Sitzungsber. d. k. Akad. d. Wiss. in Wien, mathem.-naturw. Klasse*, vol. 114, pt. 1, Feb., 1905.

[2] Wiesner, J. "Photometrische Untersuchungen auf pflanzenphysiologischem Gebiete. (I. Abhandlung.)" *Sitzungsber. d. k. Akad. d. Wiss. in Wien, mathem.-naturw. Klasse*, vol. 102, pt. 1, June, 1893; and "Untersuchungen über den Lichtgenuss der Pflanzen mit Rücksicht auf die Vegetation von Wien, Cairo und Buitenzorg (Java). Photometrische Untersuchungen auf pflanzen-physiologischem Gebiete. (II. Abhandlung.)" *Sitzungsber. d. k. Akad. d. Wiss. in Wien, mathem.-naturw. Klasse*, vol. 104, pt. 1, July, 1895.

sen and Roscoe: "Identical colors of normal papers exposed to light indicate identical products of light-intensity and time." Any tone may therefore be produced by any intensity, but reduced to a definite time, can correspond to one definite (chemical) light-intensity only.

For purposes of measurement of chemical light-intensity, a darkening of the normal paper corresponding to the normal black and brought about in one second, is considered as the unit. If, for instance, the normal black is obtained on the normal paper in 2 seconds, the light-intensity equals $\frac{1}{2}$.

By aid of this method, the light-intensity at any place, on plains, in the vicinity of buildings or groups of trees, inside of the tree-crown, in the shade, in greenhouses, in rooms, etc., can be measured. One can determine the part of the total daylight received by a plant ("relatives Lichtgenuss"), and compare this with the amount of light which, on standard paper, forms the normal tone in one second ("absolutes Lichtgenuss"). In this manner the relation between light-intensity and bud development, form of plant-body, budding and the shedding of leaves was determined. It was found that certain trees use more light than do others, that the portion of total daylight used by trees varies with the time of day, that for some trees this portion is greatest at noon, that for others it is least at the same hour.

Observations were made in Central Europe chiefly, but at times extended to 6° S. lat. and 79° N. lat. This included plains and mountain ranges in temperate climates (Central Europe), arctic regions (Spitzbergen), tropical (Java), and semitropical regions (Egypt). The extension of the experiments to high altitudes remained, more particularly a study of the change in relation between light-intensity and the amount of light used by the plant under the influence of increased altitude.

The mountainous regions of Europe do not offer a desirable field for such investigations, on the one hand because the tree-limit is reached comparatively soon, on the other because extensive plateaus at a considerable elevation above sea-level and easy of access, are lacking. Besides, on account of the numerous cañons and resulting sheltered and exposed places, introducing a vegetation of other altitudes, mixed with regressions, and causing a descent and ascent of species, the continental mountain ranges do not recommend themselves for this purpose.

The extensive American plateaus, however, offer the advantage of a gradual slope from the Atlantic to the Rocky Mountains. This is true in particular of a region beginning with the Missouri valley and

ending at the head-waters of the Yellowstone. One of the chief advantages which this section offers for photometric investigations lies in the very gradual rise of the ground from east to west, beginning with an elevation of but a few hundred meters and finally attaining a height of more than 3000 meters.

Professor Wiesner made use of these natural conditions when, in 1904, he visited the United States. Measurements were made at various points, such as Niagara, St. Paul, Colorado Springs, and Pike's Peak, but the main part of the investigation was carried on in, or in the immediate vicinity of, the Yellowstone Park, during the latter part of August and the early part of September. The medium for study was afforded by 24 herbaceous and 17 woody species.

It was found that an increase in altitude not only means an increase in the intensity of the total daylight, but also an increase in the intensity of the direct (parallel) rays as compared to the intensity of the diffused light. Earlier work[1] had shown that the amount of total daylight used by arctic plants increases as they approach the pole. Measurements in the United States showed that plants ascending to higher altitudes behave in the same manner, but only up to a certain altitude, beyond which a constantly diminishing portion of the total light is used. Evidently the increased intensity of the direct sunlight in high altitudes is not favorable to trees, as shown by the fact that plants, which at lesser elevations do not shed their leaves in summer (Hitzelaubfall), do so at greater altitudes.

A protection against the very intense direct rays is found in the cypress- (pyramid-) shape, adopted by trees in high altitudes (*Pinus murrayana* in the Yellowstone Park). Thus the rays of the midday sun strike the tree at a small angle and hence become much weakened before penetrating the crown. Trees which reach down as far as subtropical regions also have a pyramid-shaped crown, as for instance the cypress, and for the same reason, since this shape protects the trees from the too intense light from the south.

These investigations open a comparatively new field which those who live under favorable conditions will doubtless hasten to enter. The various agricultural experiment stations, for instance, could easily take up such work. In a few years there would be produced

[1] Wiesner, J. "Untersuchungen über den Lichtgenuss der Pflanzen im arktischen Gebiete. Photometrische Untersuchungen auf pflanzenphysiologischem Gebiete. (III. Abhandlung.)" *Sitzungsber. d. k. Akad. d. Wiss. in Wien, mathem.-naturw. Klasse*, vol. 109, pt. 1, 1900.

an accumulation of figures the interpretation of which would be of both scientific and practical value, being applicable to physiological and horticultural problems alike.

H. Hus

Campbell's Mosses and Ferns.[1]—This new edition of a widely used work is so much enlarged and revised as to deserve recognition as such on its title page, rather than to have it announced only in the "Preface to the Second Edition." The extent of the new matter is shown in the increase of the fourteen chapters constituting the body of the former book, by 54 pages, the addition of two entirely new chapters containing about 29 pages, and the increase of the text figures from 266 to 322. The great activity of investigators in this field during the ten years since the first edition was issued, is indicated by the addition of about 180 titles to the bibliography, while some papers referred to in the new text appear to be omitted from the list.

The portion of the text devoted to the Bryophyta is not greatly modified. The changes consist chiefly in the suppression of a few sentences here and there, and the occasional addition of a paragraph or two; *e. g.*, there is a new account of the spermatogenesis of Marchantia based on Ikeno's work. The most striking change is the elevation of the Anthocerotaceæ from the rank of a subordinate "Group" under the Hepaticæ to that of the Class Anthocerotes coördinate with the Hepaticæ and the Musci. This view is not new, for the same disposition of the group was formally made by Howe in 1899, and was followed by Professor Campbell in his *University Text-book* (1902), though neither in the latter work nor here does the author mention the fact. Little new evidence on this question is now brought forward, for the increase in the space devoted to the Anthocerotes is due chiefly to the addition of three new figures. The change has come about through the giving of greater weight to the well known peculiarities of the group, and it is to be welcomed as emphasizing the importance of these plants in phylogeny. It is a pleasure to note that the author has at last begun to adopt a consistent plan of designating orders and families in accordance with the best present usage, though it is unfortunate that he still clings to the clumsy and anomalous terms Jungermanniales Anacrogynæ and J. Acrogynæ. Incidentally

[1] Campbell, D. H. *The Structure and Development of Mosses and Ferns (Archegoniatæ)*. New York, The Macmillan Co., 1905. 8vo, vii + 657 pp., illus.

it might be remarked that the author perpetuates an error of the first edition in stating that Underwood, in substituting for the above terms the names Metzgeriaceæ and Jungermanniaceæ, regarded these families as divisions coördinate with the Marchantiales and Anthocerotes; the latter writer in fact, considered the whole group of the Jungermanniales as of equal rank with the Marchantiales.

In the portion devoted to the Pteridophyta, there is not such a consistent use of the proper ordinal terminations, and the lack of indication as to the rank of the different groups in the main headings will cause much unnecessary trouble for the student who wishes to get a general view of their relative position in classification. The most important change in this section is the removal of the Isoetaceæ from the eusporangiate ferns to a position after Selaginella. There will doubtless be general acceptance of the view that this group is sufficiently distinct to warrant the establishment of a separate order Isoetales; perhaps it might better be regarded as forming a distinct class. It is to be inferred that this may be considered Order II under the Class Lycopodineæ (as in the *University Text-book*), but the author makes no statement on this point, and his rather detailed emphasis on the facts pointing to "a real, but extremely remote relationship between Isoetes and the Eusporangiatæ" may leave the student in doubt as to why this genus is generally connected with the Lycopods. There are many important additions to text and illustrations, particularly in such recently investigated forms as Botrychium, Selaginella, and Isoetes.

One of the new chapters, on "The Nature of the Alternation of Generations," champions the antithetic theory with the same general argument as that advanced by Professor Campbell in the *American Naturalist* in 1902; he considers that the advocates of the homologous theory have not furnished sufficient evidence to substantiate their view. Here as well as elsewhere, the author gives some prominence to Coleochæte as the probable ancestor of the bryophytes. The recent investigations of Allen on chromosome reduction in this genus indicate, to say the least, that it is much further removed from the bryophytes than has been supposed. We should be unwilling to say there is no alternation of generations in Coleochæte; but if the phenomena of reduction are to be made the chief means of interpretation, the sporophyte is undifferentiated, consisting only of the fertilized oöspore, while the first four cells produced in its germination, or possibly the mass of loosely connected cells, may bear a remote comparison to the spores of mosses. Certainly the view held by Campbell and others

that the zoöspores produced by these cells are homologous with the moss spores was not rational; for that zoöspore production is only one method of germination of these cells, depending upon accidental conditions, is proved by the fact that they may grow out directly into filaments, as shown by Chodat and others.

The other new chapter furnishes a convenient but necessarily brief and incomplete *résumé* of the fossil Archegoniates. In the concluding chapter, the author holds mainly the same views as previously: he is inclined to believe that the Spermatophyta are polyphyletic in origin, since the Conifers show the greatest resemblance to the Lycopodineæ, and the Cycads to eusporangiate ferns (through the Cycadofilices); while the Monocotyledons may possibly be derived from aquatic ancestors resembling Isoetes, and the Dicotyledons from the Monocotyledon stock.

There are numerous paragraphs in the first edition where the language is obscure, and we have hoped in vain that these might be made more clear for the benefit of the student who can ill spare time to dig out their meaning. Nevertheless in spite of these and some other defects which might have been remedied without very great labor, it must be said that Professor Campbell has given us a much improved and more usable edition of a valuable book.

T. E. Hazen

Common and Conspicuous Lichens of New England[1] is the title of a series of booklets by R. H. and M. A. Howe. The descriptions are accompanied by some very good photographic reproductions of the lichens in their habitats, as well as by line drawings of the thallus. The work is being issued in parts. Part I contains twenty-two pages; Part II, eighteen pages. The following genera are described in the first two parts — Ramalina, Cetraria, Evernia, Usnea, and Alectoria.

H. S. R.

Czapek's Biochemistry of Plants.[2] — Each year witnesses an increasing interest in the study of biological chemistry. As time goes on the work becomes broader and yields more results. Until recently the subject would have perhaps been more aptly designated as zoö-

[1] Howe, R. H., Jr., and M. A. *Common and Conspicuous Lichens of New England; a Fieldbook for Beginners.* Boston, W. B. Clarke and Co., 1906. 16mo, Parts 1, 2, 40 pp. $1.00

[2] Czapek, F. *Biochemie der Pflanzen.* Jena, Bd. 1, 8vo, pp. xv + 584, 1904; Bd. 2, 8vo, pp. 1186, 1905.

chemistry, since most of the investigators busied themselves with the physiological chemistry of animals. Indeed, the term *physiological chemistry* itself is usually understood to deal with the study of animal tissues. Happily, this field which has yielded so richly to the zoölogists, is beginning to be explored more widely by the botanists.

The appearance of Czapek's work marks the beginning of an epoch which should mean much for future work in plant physiology and, indeed, in all other lines which are in any way concerned with the chemistry or physiology of the plant. The author is a well trained botanist, physiologist, and chemist. He gives the reader a truly broad and modern view of the subject in hand, the book being in all senses of the word a *biological* chemistry of plants, not a chemistry of plant organs or plant products. Throughout the entire work, we find the literature on every subject summarized and brought down to date with almost unparalleled accuracy and completeness.

The first volume opens with a brief but comprehensive historical introduction. The General Part treats in a very fundamental manner the physical and chemical processes underlying all vital phenomena. Especial attention is given to the characteristics of colloids, to the general chemistry of enzymes, and to the nature of chemical action in the same.

The Special Part opens with a chapter on the fats and lecithins. Their distribution, metabolism, and storage in plants are made topics of especial interest. In discussing the *rôle* of lecithins, the author shows reluctance in accepting any of the theories which assign to them special *rôles*.

The chemistry and occurrence of the sugars is the subject of a very complete discussion occupying some forty pages. This discussion opens the way for the author's extended treatment of carbohydrate metabolism in the plant. He first treats of the storage of carbohydrates and food value in fungi, bacteria (including alcoholic and other fermentations), seeds, and subterranean storage organs. Then he discusses with great fullness the carbon assimilation of the green organs of plants. Naturally, his treatment is too extensive to be set forth adequately in a review paragraph. Suffice it to say that the author brings together the results of the best work on that subject and discusses it fully from the standpoint of chemistry and biology. The carbohydrates are treated from their origin in the plant to their storage as reserve products in various storage organs.

Following the above subject in quite a logical manner comes the study of the cell wall of the plant. First comes the unmodified cellu-

lose wall of simple plants or plant organs, then the hemicelluloses, pectins, and pentosans, and finally the chemical and physical changes which walls undergo. With these considerations the first volume closes.

The second volume continues the treatment of chemosynthetic activity. More than two hundred pages are devoted to the proteids. Our knowledge of the general chemistry of vegetable proteids and of proteolytic ferments is comprehensively written up and revised to the end of the year 1904. The proteid metabolism of the bacteria, fungi, ripe seeds, seedlings, etc., is given separate treatment. In successive chapters the discussion takes up the proteid bodies, their cleavage by ferments, absorption of the products by the plant, and formation of reserve proteids.

One is gratified to find that the author sets forth at some length the elucidating theory of proteid chemistry based upon the amino-acid constitution. Since this new theory promises to clear up the "mysterious" structure of the "awful proteid," it is proper that it receive a prominent place in any comprehensive work on biochemistry.

The pyridin and chinolin bases are given very full treatment in the discussion of alkaloids.

The phenomena of respiration, fermentation, and oxidizing enzymes are made the principal topics of a long and interesting chapter on the absorption of oxygen by plants. Here, as elsewhere, the author brings out with force and clearness the chemical basis of the activities of living matter. Naturally, the oxidation of carbohydrates and the distribution and constitution of the resulting vegetable acids receive extended treatment at this place. The author is inclined to support the view of Neubauer, that the vegetable acids have the function of neutralizing the inorganic bases which are formed in ripening fruits. The great mass of literature on oxidizing enzymes is carefully brought together and arranged in an orderly manner. The author points out that in many studies of oxidases sufficient care has not been used to exclude other enzymes.

The discussion of "omnicellular cyclic carbon compounds" is largely devoted to quinone, phenols, and tannin. Czapek contends that the concept of "tannin," as used in botany, is altogether too loose, this name being applied to any substance which turns black upon the addition of iron chloride, but many substances like vanillin and morphine react with iron like tannin. He probably sets forth the true estimate of tannin when he shows that it does not perform any one but a variety of functions in the plant.

One hundred and seventy pages are devoted to the *rôle* of the mineral elements in plants. It is probably safe to say that never before has this subject been so scientifically treated, nor has such a wide range of analyses been collected into one work. In no other part of the work does the author show greater breadth of mind and freedom from provincial ideas than in dealing with this oft-debated subject. The discussion treats in separate chapters the *rôle* of the elements in bacteria and fungi, in seeds, in subterranean storage organs, in buds, in the wood of trees, in the bark of trees, in leafy organs (including mosses and ferns), in algæ, in pollen grains, in fruits, and in roots. Not merely are many tables of analyses given, but there is discussion upon the probable value and function of each element to the plant. Much discussion is given to the probable *rôle* of elements like calcium and magnesium, on which much work has been done. In the particular case of these elements, the author brings together the results of a large number of workers with great justice and precision. The work of Loew is naturally given much prominence, yet he thinks that that author has not in all cases taken a sufficiently broad view of the facts, since too great importance is undoubtedly attached to the antagonism of calcium and magnesium.

The last chapter of the book is devoted to a discussion of the responses of plants to chemical stimuli. Under different headings there is brought together the work on the stimulation of protoplasmic streaming; the stimulation of nuclear and cell division; the stimulation of growth by toxic substances; the formative effect of chemical stimuli upon vegetative and reproductive organs.

The book is indispensable to all workers in physiology, whether of plants or animals, as well as in physiological and organic chemistry.

H. S. R.

Lacouture's Liverworts of France.[1] — This elaborate monograph takes the form of a synoptical key which is arranged in three series of tables; the first gives the characters of the tribes, the second of the genera, and the third of the species. Seventy-five genera containing two hundred and twenty-five species are described.

The characters upon which the classification rests are almost entirely those of the vegetative structures, and they are minutely depicted.

[1] Lacouture, Ch. *Hepatiques de la France. Tableaux synoptiques des caractères saillants des tribus, des genres et des espèces.* Paris, P. Klincksieck, 1905. 4 to 77 pp., 200 figures.

The description of each species is accompanied by a distinct figure showing the characteristics of the plant, especially those upon which the classification is based.

Several new genera are created by raising subgenera to the rank of genera. Jungermannia is divided to form the genera Sphenobolus, Lophozia, and Aplozia; likewise, Riccia is divided to form three genera, Ricciocarpus, Ricciella, and Euriccia; Cephalozia, to form Eucephalozia and Cephaloziella.

The work is one which will prove to be very valuable, and it will be particularly useful in classifying material which does not possess the organs of fructification.

H. S. R.

(*No. 475 was issued July 11, 1906*)

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CONTENTS

			Page
I.	Histogenesis of the Retina	PROFESSOR A. W. WEYSSE AND W. S. BURGESS	611
II.	Notes on Marine Copepoda of Rhode Island	L. W. WILLIAMS	639
III.	Lichens of Mount Monadnock, New Hampshire	R. H. HOWE, JR.	661
IV.	Notes and Literature: *Botany*		667
V.	Publications Received		677

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THE

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HISTOGENESIS OF THE RETINA[1]

ARTHUR W. WEYSSE AND WALDO S. BURGESS

INTRODUCTION

THE histology of the vertebrate retina has been carefully investigated in several animals and the adult structure of that organ is now fairly well understood, but the development of the retinal elements has received very little attention. The literature on the eye deals chiefly with the formation of the optic vesicles and with the histology of the adult organ. The only writer who has attempted to follow out the histogenesis of the retinal elements appears to be Cameron (:05) in a series of papers on the development of the retina in Amphibia, while Bernard (:00–:04) has given some attention to the development of the rods and cones. The investigations on which the present paper is based, were made on the retina of the chick. This animal was selected for study, first because it has never been investigated before, and second because it affords so readily a complete series of stages of development so that there need be no gaps for lack of material. Since it has been necessary to compare the results obtained here with those of Cameron, his technique has been followed closely, but in addition certain modifications of it have been used, for while in many cases by using his methods results precisely similar to his have been obtained, yet by other methods results more in accord with the known processes of cell and tissue development in other organs of the body have been secured.

[1] From the Biological Laboratory of Boston University, College of Liberal Arts.

TECHNIQUE

In the course of this work several fixing reagents have been tried with varying degrees of success. Of these, Kleinenberg's picrosulphuric mixture has proved entirely satisfactory in most cases, but the best results have been obtained from the fluid used by Cameron and known as the Bles fluid; it is made as follows:—

70 % alcohol	90 parts
Glacial acetic acid	3 "
Commercial formalin	7 "

The embryos remained in this for one week and were then transferred to 70% alcohol.

When needed, the eyes were dissected out, cut in halves by a vertical section through the optical axis, and placed in 90 % alcohol for three hours, followed by 95 % alcohol for from six to twelve hours according to size. They were then cleared in cedar oil and finally imbedded in paraffin, being passed through two paraffin baths of one and three hours each, kept at a temperature of 53° C.

All sections were made with a Bausch and Lomb sliding microtome and mounted in the usual way. All were stained on the slide.

In most cases two different staining methods were used in each stage of development for the sake of comparison. These were a 33 % aqueous solution of Delafield's hæmatoxylin followed by an alcoholic solution of eosin, and an iron-alum preparation described by Cameron.

This second method gave entire satisfaction in every respect when modified by the subsequent use of eosin. The slide was first placed in a 4 % aqueous solution of iron-alum, the violet-tinted crystals, and allowed to remain ten minutes. This treatment acts as a mordant of course. It was then thoroughly washed in tap-water, dipped in a saturated aqueous solution of hæmatoxylin for ten minutes, and again washed in water. This left the sections jet black. The slide was then placed once more in the iron-alum solution and carefully watched until the sections were of a light purple tint. They were then rinsed in water and

examined under the microscope. If over-stained they were bleached a little longer in the iron-alum, if not stained enough the hæmatoxylin was repeated. The process has the advantage that it admits of absolute control. The slide was next placed in an alcoholic solution of eosin for about fifteen seconds and the excess of stain washed out in alcohol. An oil-immersion lens is absolutely essential for making out the details of retinal development.

Earlier Stages of Retinal Development

After the primary optic vesicle has invaginated to form the secondary optic vesicle or optic cup, as shown in Fig. 1, it is readily seen that the invaginated portion, the earliest stage in the development of the retina, and the uninvaginated portion, which is continuous with it and is to become the pigment layer, consist of nuclei essentially similar in structure, with more or less granular protoplasm about them,—the two layers differing in thickness only. Karyokinesis at this stage takes place at the margins only of the optic cup, in both the retinal and the pigment layers.

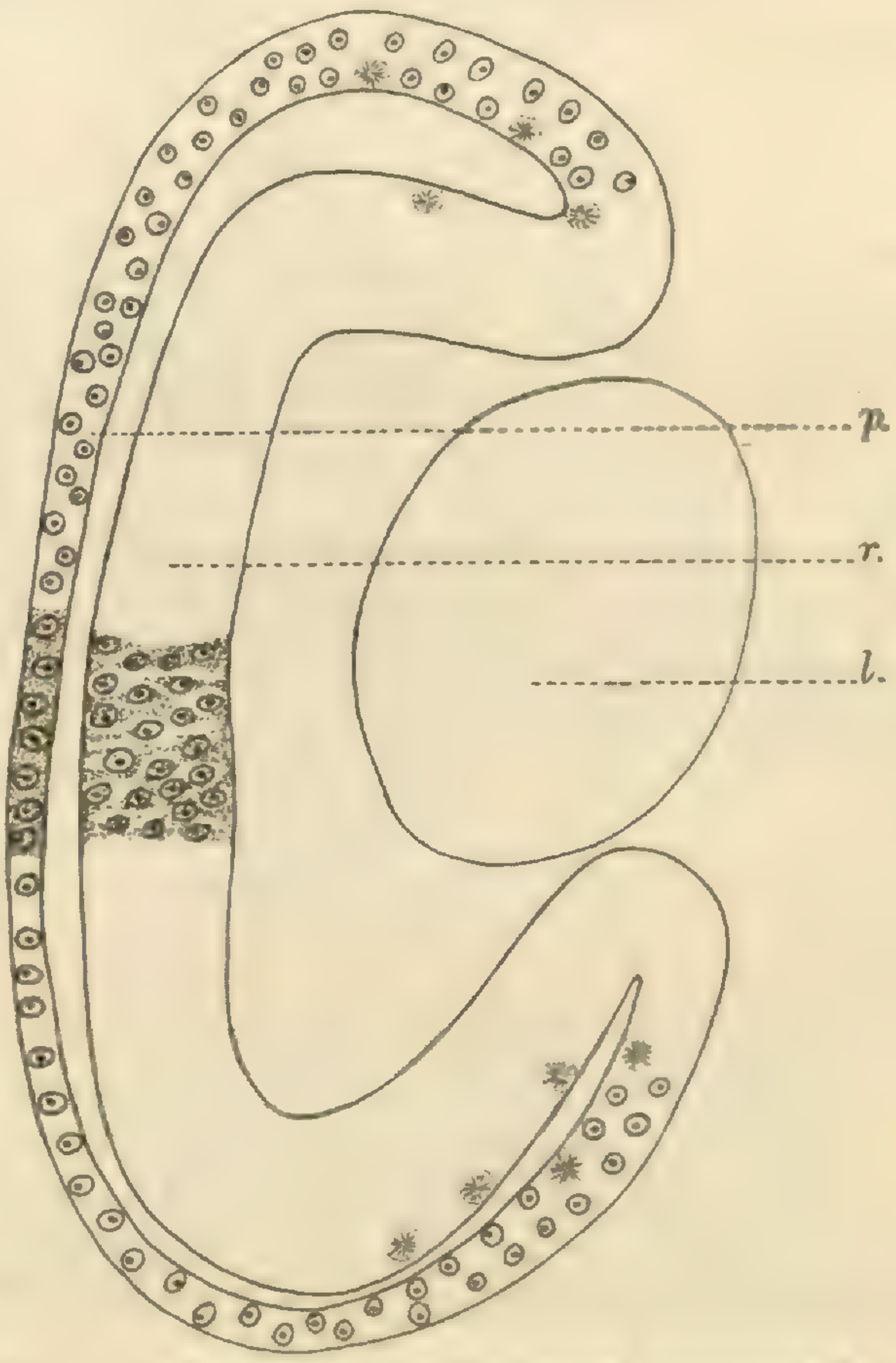

Fig. 1.— Section through the entire optic cup of a 64 hours' embryo showing relative distribution of the nuclei in the pigment layer and the retina; the mitotic figures indicate the only points at which karyokinesis takes place at this stage of development. x 220. *l.*, lens; *p.*, pigment layer; *r.*, retina.

In the earliest stage in which the retina as such is to be identified, its structure consists of nuclei suspended in cytoplasm without cell

walls, *i. e.*, it is a syncytium whose outer and inner extremities form the external and internal limiting membranes. This is in accord with the conclusion of Bernard (:00). Early writers described it as made up of discrete cells, while Cameron goes to the opposite extreme and maintains that it consists of nuclei with absolutely no cytoplasm at all. Cytoplasm there certainly is in the chick at this stage if a cytoplasmic stain is used, but it is almost impossible to demonstrate it with a nuclear stain alone. It is difficult, however, to determine just what or how much cytoplasm is to be associated with each nucleus since cell walls are absent. The nuclei are evidently all alike except for slight differences in shape, some being elliptical and some circular in outline; this may be due to their being cut in different diameters. The first measure 7.29 μ by 4.38 μ, while the second are 5.83 μ in diameter. This is as large as any retinal nuclei ever become.

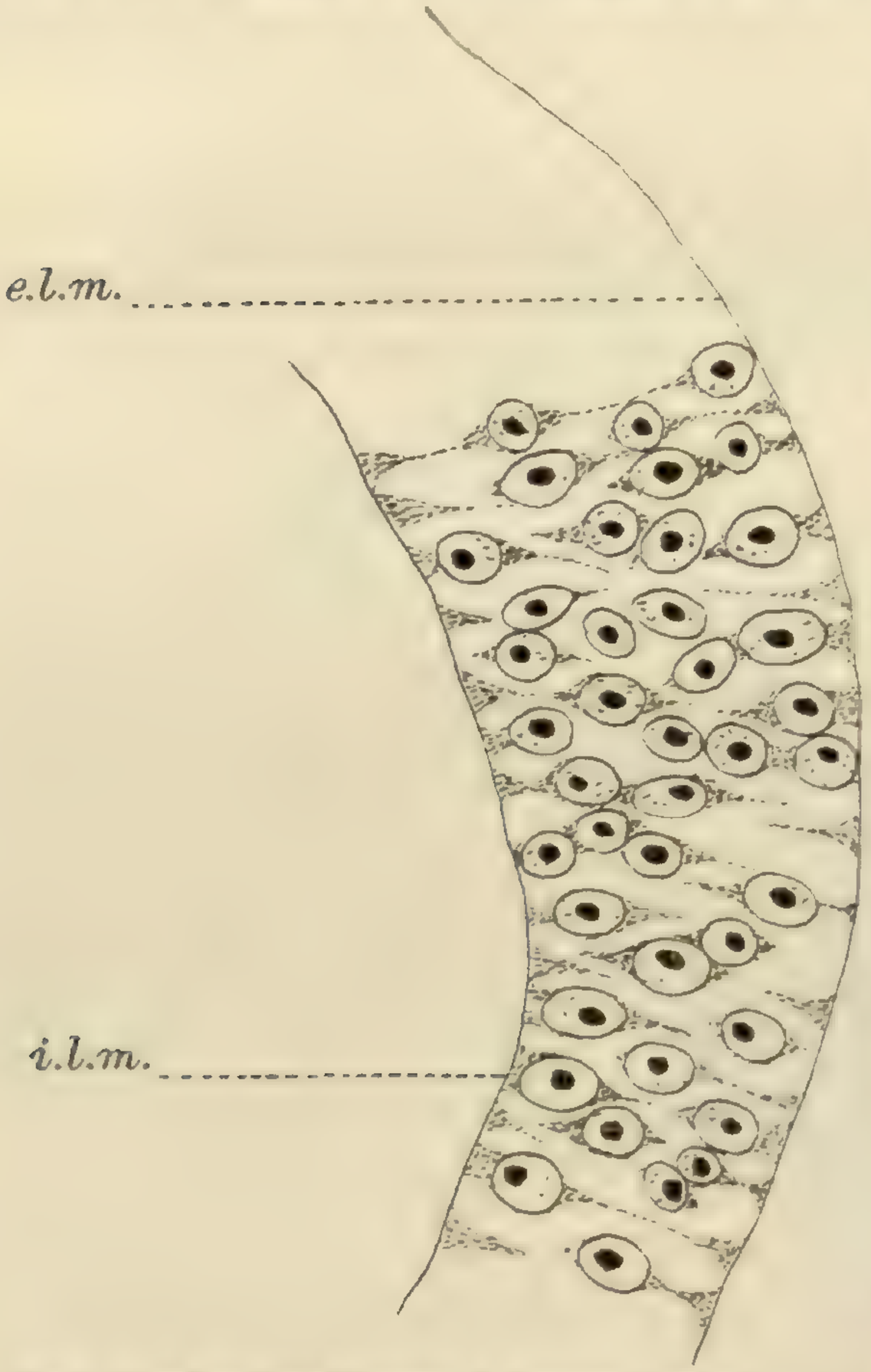

FIG. 2.— Section through a portion of the retina of a 56 hours' embryo. Each nucleus is provided with cytoplasm at its inner and outer ends. There is no cell division going on at this point in the retina at this stage. x 810. *e. l. m.*, external limiting membrane; *i. l. m.*, inner limiting membrane.

Although no structural difference is apparent, there is, however, an intrinsic difference in these nuclei. Those next the external limiting membrane have the power of division, while the others have not. These then may be called the row of germinal nuclei, which at this early stage are not dividing except at the junction of the retina with the pigment layer, but division begins immediately after the complete formation of the optic cup, so that karyokinetic figures are found from margin to margin until the beginning of differentiation of the retinal layers.

The dividing nucleus is surrounded by a clear, fluid-filled space several times as large as the other nuclei. Its outline, though formed by the surrounding protoplasm, is so pronounced as to simulate closely the appearance of an enveloping membrane. This is well shown in Fig. 5.[1] In the one in the center the plane of the section passes through the long axis of the spindle, while in

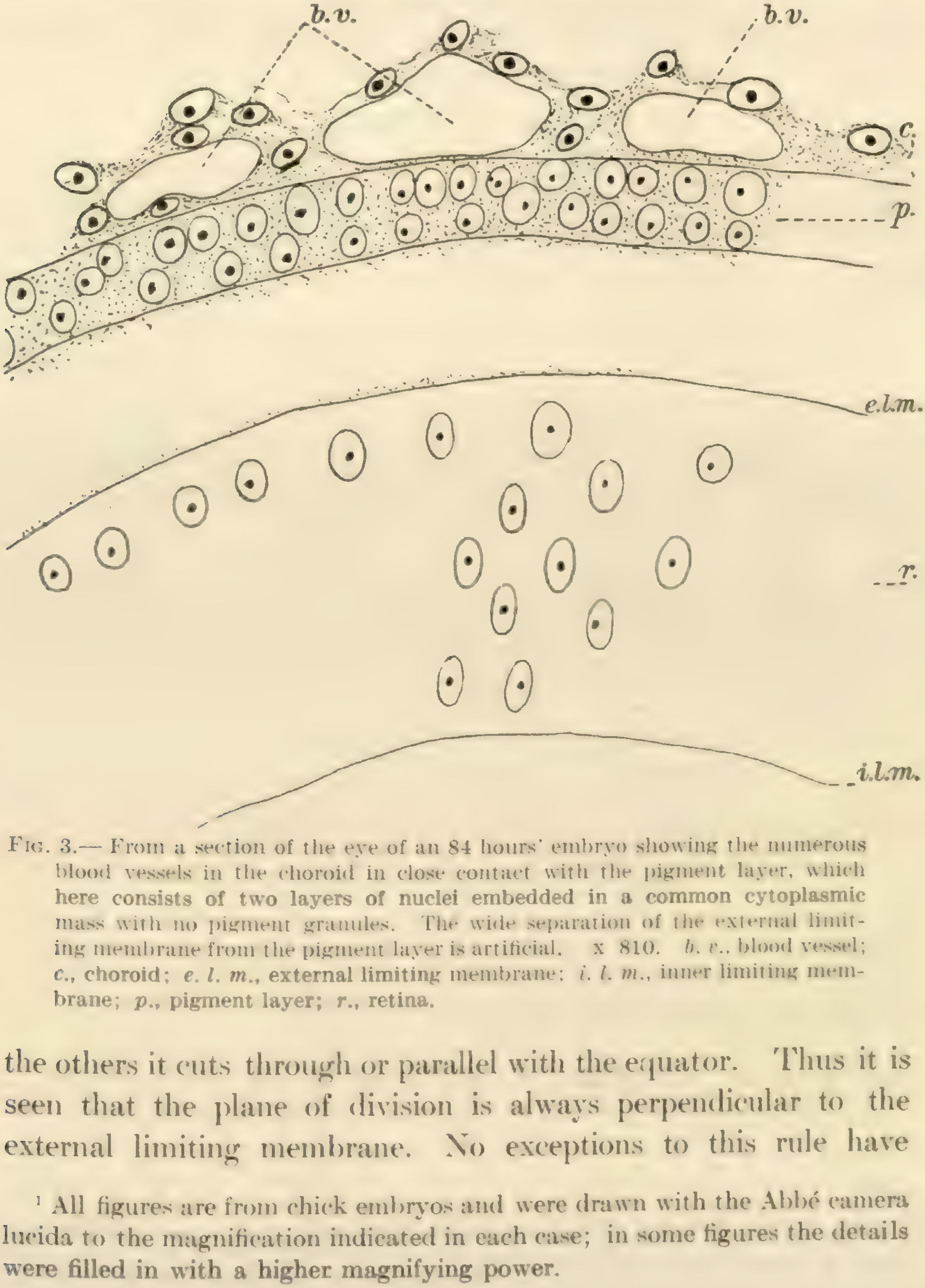

FIG. 3.— From a section of the eye of an 84 hours' embryo showing the numerous blood vessels in the choroid in close contact with the pigment layer, which here consists of two layers of nuclei embedded in a common cytoplasmic mass with no pigment granules. The wide separation of the external limiting membrane from the pigment layer is artificial. x 810. *b. v.*, blood vessel; *c.*, choroid; *e. l. m.*, external limiting membrane; *i. l. m.*, inner limiting membrane; *p.*, pigment layer; *r.*, retina.

the others it cuts through or parallel with the equator. Thus it is seen that the plane of division is always perpendicular to the external limiting membrane. No exceptions to this rule have

[1] All figures are from chick embryos and were drawn with the Abbé camera lucida to the magnification indicated in each case; in some figures the details were filled in with a higher magnifying power.

been observed. After each division into two, one nucleus is left behind to contribute one additional row to the thickness of the retina while the other grows to its original size and divides again. Thus the external limiting membrane is continually moving outward the width of a nucleus with each successive generation of germinal nuclei. The fate of the nuclei thus left behind will be considered in connection with the various retinal layers.

Differentiation begins at the time the majority of germinal

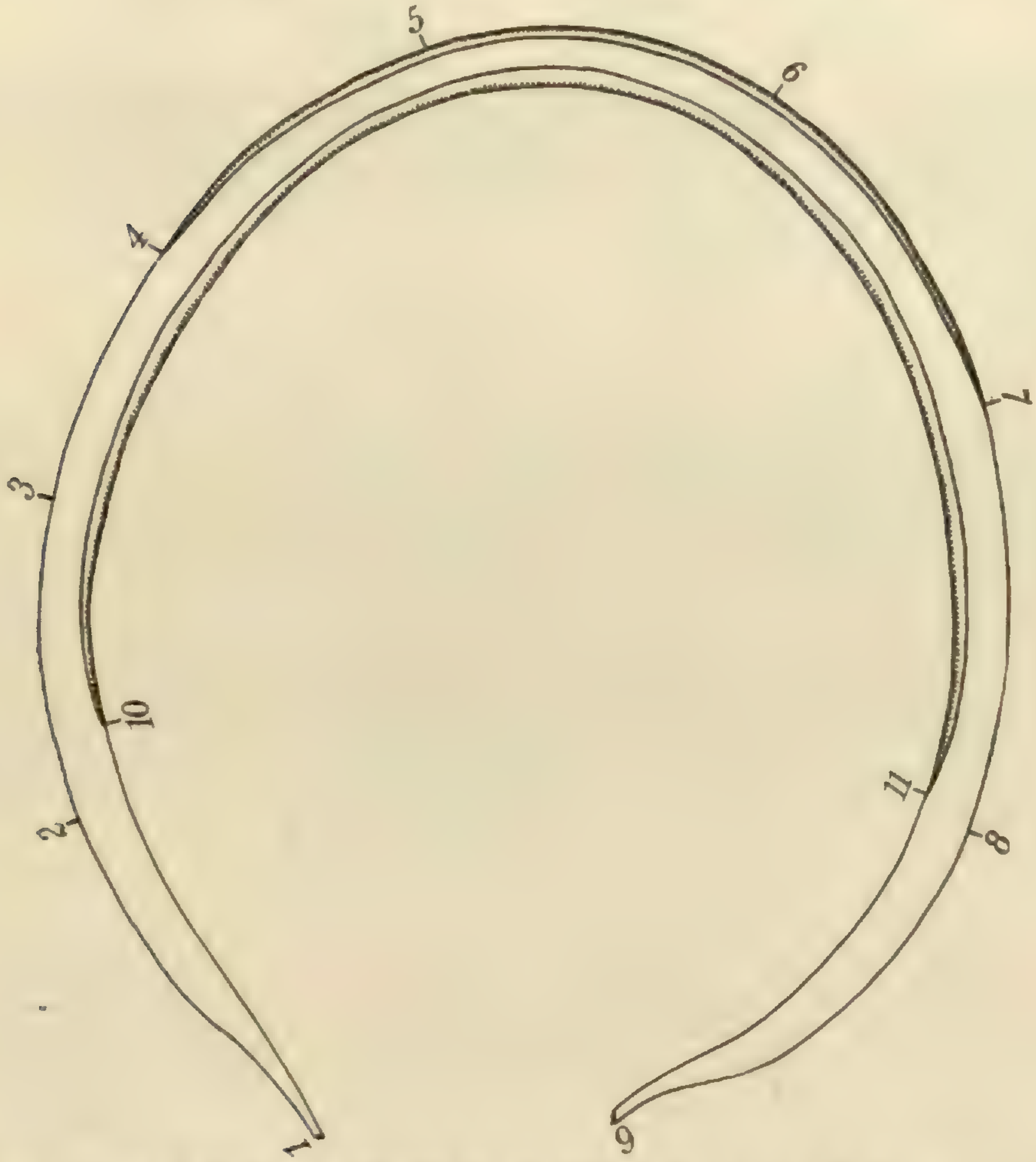

FIG. 4.— Outline drawing of a section of the entire retina of a 7¾ days' embryo. The layer of rods and cones and the outer reticular layer extend from IV to VII. The ganglion-cell layer and the inner reticular layer extend from X to XI. In the layer of germinal cells the numbers of nuclei in a dividing stage are as follows: from I to II, 82; from II to III, 47; from III to IV, 32; from IV to V, 17; from V to VI, 5; from VI to VII, 23; from VII to VIII, 56; from VIII to IX, 80. x 19.5.

nuclei at the center of the retinal cup cease to divide, that is, at the end of the period of most rapid growth. Commencing thus at the center it gradually encroaches upon the territory of

the undifferentiated margins. In this way every section contains in its various parts all the preceding stages through which it has passed. For instance a segment near the margin of a ten days' retina would have attained the same degree of development as a segment through the center of the retinal cup from a younger eye. Hence in the discussion of development in this paper it is always the most highly developed portion of the retina, the center, on which all conclusions are based, and not the parts nearer the margin, which invariably represent an earlier stage.

In the growth of the retina as a whole there are three well defined periods: (1) the period of cell-multiplication, (2) the period of readjustment, (3) the period of final differentiation. The first, which extends from the second to the eighth day, is characterized by a tremendous increase in the number of nuclei and consequently in a rapid growth in the size and thickness of the whole retina, which at the end of this stage has attained its maximum width of 195 μ. During the succeeding period of readjustment, from the eighth to the tenth day, there is still a rapid growth at the margins, but at the center of the retinal cup the number of nuclei is henceforth practically fixed, and the principal change is that of redistribution or readjustment into layers. Incidental to this there is a sudden decrease in width to 150 μ, undoubtedly due to a stretching out of the surface area. The stage of differentiation, extending from this time to the end of incubation, is marked by the growth of cytoplasmic processes and by a gradual increase to 180 μ in the thickness of the retina.

The Ganglion-cell Layer

The ganglion-cell layer is the first to appear with the beginning of the period of readjustment, as shown in Fig. 6. It consists at first of three rows of nuclei which are marked off from the others by the commencement of the inner reticular layer. As the surface area of the retina increases, these nuclei, whose number of course remains the same,[1] gradually fall into line, beginning at the center

[1] In a $7\frac{3}{4}$ days' embryo a single dividing nucleus was found in this layer, the only exception in the entire series studied.

of the retinal cup and thence radiating outwards on every side toward the margins, until at the end of this period the layer comes to be composed of a single phalanx of nuclei (Fig. 7). This readjustment takes place in the direction of the internal limiting membrane as is shown by the fact that there is no corresponding increase in the width of the nerve-fiber layer. Thus in its development the ganglion-cell layer actually decreases in width from 28.6 μ to 10.4 μ.

Part of the nuclei of this layer are the same nuclei that were seen in the early retina immediately after the formation of the optic cup (Fig. 1), and the remainder are the first nuclei to be formed by the division of the germinal nuclei. All are of the same size as those found in the early undifferentiated condition; that is to say, after division each nucleus grows to the size of the parent nucleus, a fact also true of the amacrines or horizontal nuclei. At the advent of the third stage of growth, with its attendant increase in the amount of cytoplasm, these cells become multipolar and gradually approach nearer and nearer the condition of the adult retina.

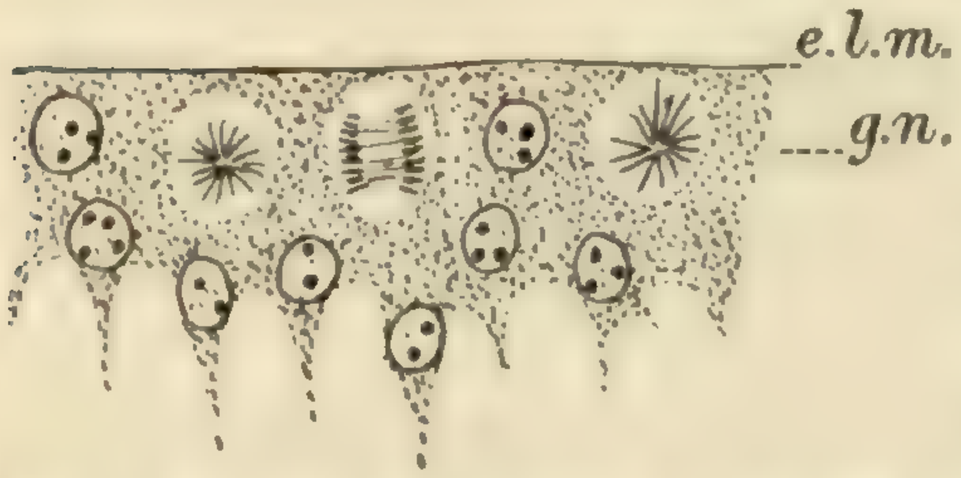

FIG. 5.— Germinal nuclei in process of division,— from the retina of a 6½ days' embryo. All the nuclei are imbedded in a mass of granular cytoplasm, and in each case the cleavage plane is at right angles to the external limiting membrane. x 1500. *e. l. m.*, external limiting membrane: *g. n.*, germinal nuclear layer.

THE INNER NUCLEAR LAYER

The inner nuclear layer, which is by far the largest and most conspicuous of all, has its beginning in the fourteen successive generations of nuclei immediately following the production of those which are eventually to become the ganglion cells. Fig. 12 shows this layer in the process of formation and Fig. 13 gives the appearance three fourths of a day later. It does not become a complete layer by itself until the beginning of the period of readjustment when the outer reticular layer appears and separates it from the future external nuclear layer; but long before this, differentiation has already taken place.

In this layer the nuclei of the first generation become the inner horizontal cells while the nuclei of the last generation become the outer horizontal cells. In both cases, as mentioned before, these nuclei after division grow to the size of their immediate ancestors, the early germinal nuclei. This, however, is not true of the intermediate generations. Here each successive phalanx fails to attain quite the size of the one preceding, so that when the process is complete we get the effect of a gradation of nuclei apparent in Fig. 15, where they range in size from 5.83 μ to 4.38 μ in diameter.

FIG. 6.—Section through the retina of a 7¾ days' embryo. The ganglion-cell layer here consists of three layers of nuclei and the inner reticular layer has just begun to form. Nuclei are still dividing in the germinal layer, and the pigment layer is connected with the external limiting membrane by cytoplasmic strands. x 440. *b. v.*, blood vessel; *e. l. m.*, external limiting membrane; *g. c.*, ganglion-cell layer; *i. l. m.*, inner limiting membrane; *i. r.*, inner reticular layer; *m. f.*, radial fibers of Müller; *n. f.*, nerve-fiber layer; *p.*, pigment layer.

During the first two periods of growth the nuclei of this layer, which measure 7.29 μ by 2.92 μ on an average, are all extremely elliptical in outline, with the long axis at right angles to the limiting membranes. When examined with a low magnifying power they appear sharply pointed at the ends, and Bernard (:04) has figured them thus in his Plate 29, Fig. 25. But when studied with the oil immersion these nuclei are seen to be elliptical and bounded by a very distinct membrane which is rounded at the ends. They present very much the appearance of having been pulled outward toward the layer of germinal nuclei, for the cytoplasm about them streams from each pole in the direction

of the limiting membranes. Some of these nuclei, especially those near the middle of the layer, eventually become supporting cells or fibers of Müller. This is well shown in Fig. 12. Up to the end of the period of readjustment the chromatic substance of all retinal nuclei is scattered about in the nucleus as several granules; later, there is a single large, clearly defined chromatic mass. This condition appears to be true of other embryonic tissues as will be seen by the figure, but it is especially evident in these elliptical nuclei of the inner nuclear layer.

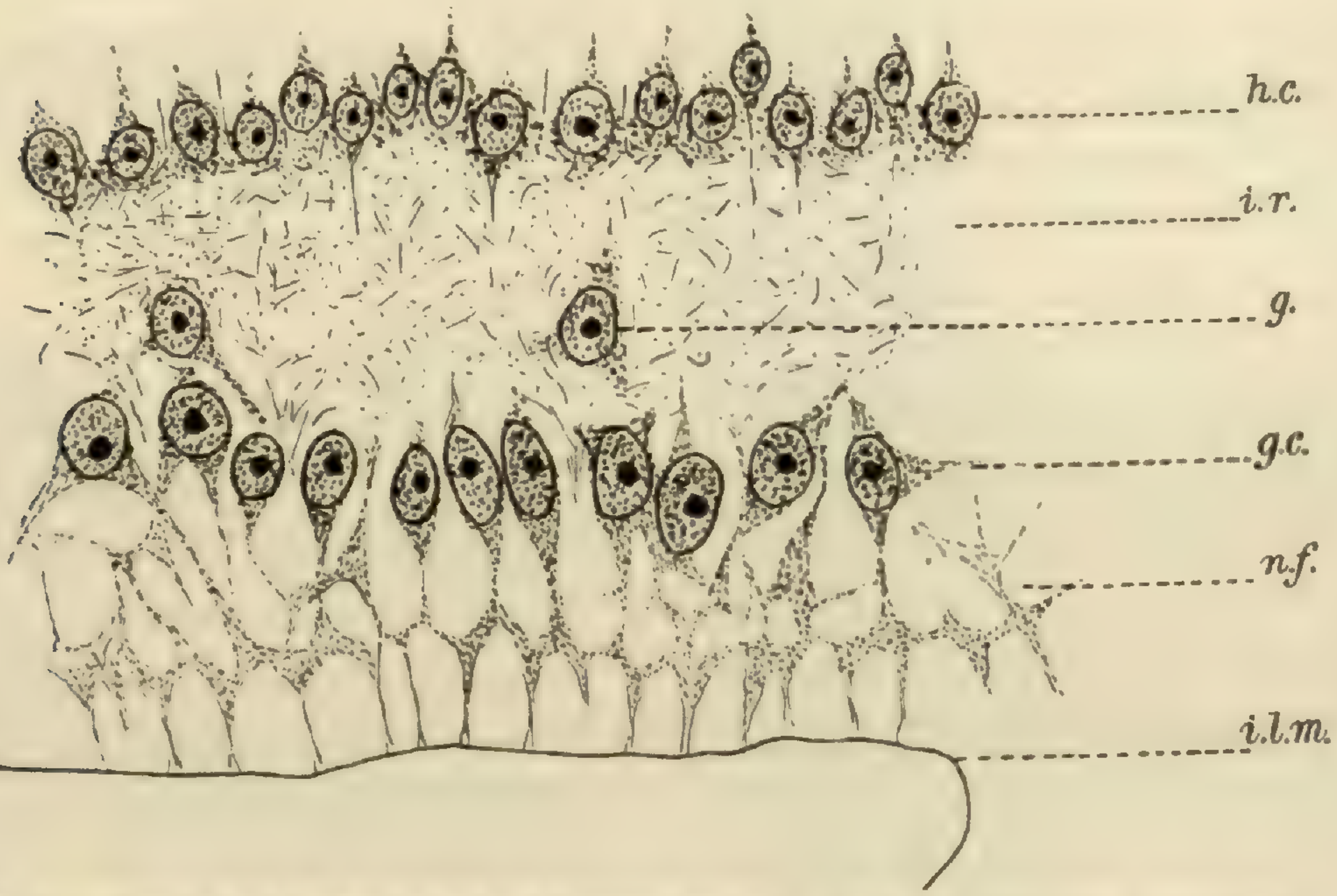

FIG. 7.— Portion of the retina of a 10 days' embryo. The ganglion-cell layer now consists of two layers of nuclei. The inner reticular layer is well differentiated and the adjacent nuclei of the inner nuclear layer will develop chiefly into horizontal cells. x 810. *g.*, ganglion cell; *g. c.*, ganglion-cell layer; *h. c.*, horizontal cells or amacrines; *i. l. m.*, inner limiting membrane; *i. r.*, inner reticular layer; *n. f.*, nerve-fiber layer.

To account for the enormous increase in the number of these nuclei in so short a period two explanations have been advanced: the theory of migration and the theory of direct division; neither of these appears to us probable. The first is advanced by Bernard (:00–:04). He states that in order to account for this rapid increase in numbers "we have to assume a stream of nuclei from the undifferentiated edges of the retina towards the base of the cup." In another place in the same paper he asks the question: "Where does the middle nuclear layer get its supply of nuclei to furnish

the outer nuclear layer?" Our work on the chick demonstrates clearly that the outer nuclear layer is not derived from the inner nuclear layer in any sense of the word. Each layer is first laid down by successive generations of nuclei from within outward as Fig. 12 shows. As before stated this process is followed by a later readjustment in each layer, but not by migration from one layer to another. As for Cameron's theory of direct division there is absolutely no evidence that such a process takes place in the chick. Even at the center of the retinal cup mitotic division does not wholly cease until nearly all the rods and cones have reached an advanced stage of development.

From the time the outer reticular layer begins to appear at the end of the first period of growth no more nuclei are added to the inner nuclear layer. It has then attained its maximum thickness of

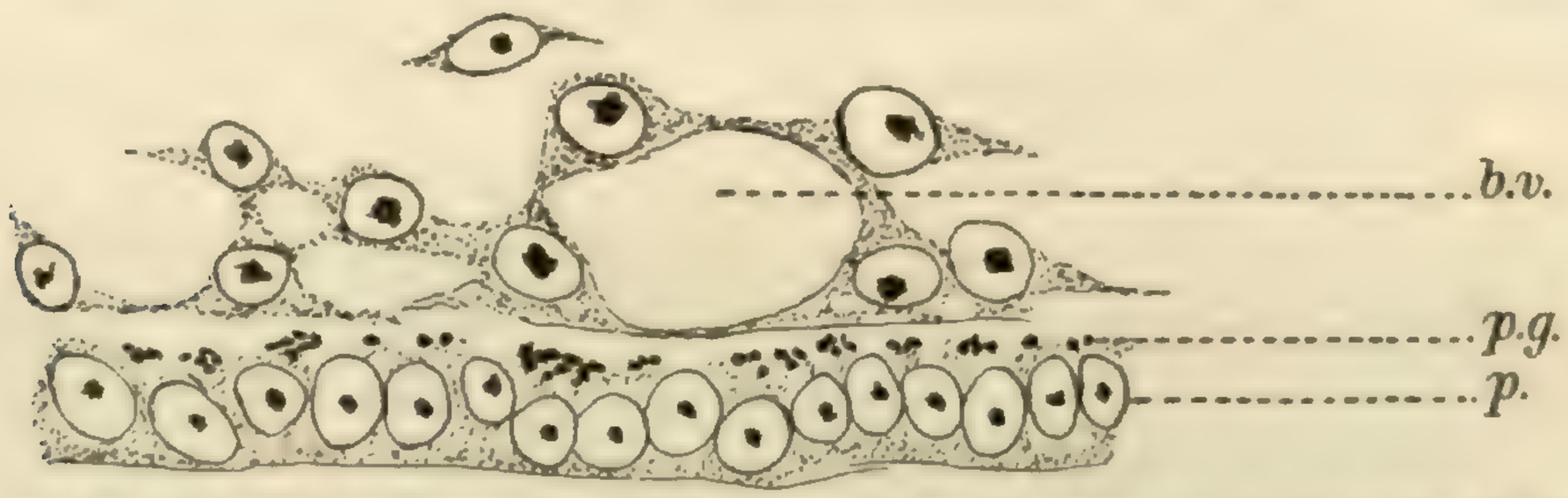

FIG. 8.— An 88 hours' embryo, in which pigment granules appear in the outer portion of the pigment-layer cells; the nuclei of this layer are closely packed together. x 810. *b. v.*, blood vessel; *p.*, pigment layer; *p. g.*, pigment granules.

111.8 μ. The nuclei are all crowded very closely together, this being especially true of the half of the layer nearer the external limiting membrane. Then begins the period of readjustment, during which the layer diminishes in thickness to 65 μ. With the stretching out in area of the whole retina and its consequent restoration of equilibrium or equalization of tension, if we may so express it, the nuclei become more loosely arranged and gradually assume the circular outline, Figs. 13 and 15. The number of phalanges, or rows of nuclei, which was at first fourteen, has now decreased to eight, for there has been a gradual closing up of the ranks in the direction of the external limiting membrane, made evident by the corresponding increase in the width of the inner reticular layer.

In the final stage of differentiation there is little change in this

layer except for a slight decrease in thickness from 65 μ to 44.2 μ. The nuclei stain more deeply with the iron-alum hæmatoxylin, and all are spherical except those of the supporting cells or fibers of Müller, while the nuclei of the horizontal cells are readily distinguished by their clearer texture. The cytoplasm of the layer remains the same in amount and appearance as at the beginning.

THE RETICULAR LAYERS

The reticular layers are purely cytoplasmic in both origin and structure, there being no evidence to the effect that nuclei have anything to do with their formation. Each retinal nucleus, except in mitosis, is always enveloped in an intact nuclear membrane, and there are never appearances that might suggest the extrusion of nuclear substance or in the strict sense of the word the protrusion of processes of any kind. To be sure, the cyto-

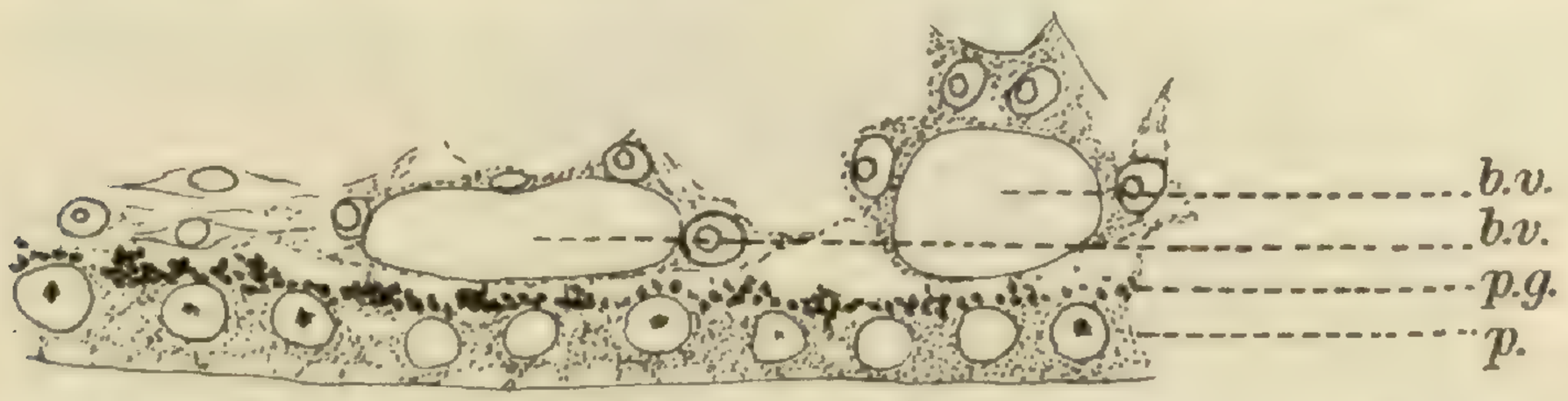

FIG. 9.— A 7 days' embryo; the nuclei of the pigment layer are more widely separated from each other; the pigment granules are more numerous and still entirely on the outer side of these nuclei. x 810. *b. v.*, blood vessel; *p.*, pigment layer; *p. g.*, pigment granules.

plasmic processes of the bordering nuclei eventually extend into these layers to varying depths, but there is no ground for the assumption that such cytoplasm is of nuclear origin as Cameron believes is the case in the frog.

The inner reticular layer, which is the first of these to form, begins to appear at about the middle of the period of cell multiplication. It starts as a narrow protoplasmic rift between the third phalanx of the early ganglion-cell layer and the first generation of nuclei in the future inner nuclear layer (Fig. 6). This rift gradually widens, a little in the direction of the ganglion-cell layer, but chiefly toward the inner nuclear layer as these two layers develop. Viewed as a whole the layer has in section a crescent-shaped outline, and as it develops the pointed edges of

the crescent encroach more and more upon the undifferentiated margins, as seen in Fig. 4.

The rate of development of this layer is fairly uniform from the time of its first appearance to the end of incubation. At the commencement of the period of readjustment it has attained a width of 13 μ, which has increased to 18.2 μ at its close. As will be remembered, it is during this time that the ganglion-cell nuclei fall into line, hence some of these stragglers are still to be seen lingering behind in this layer (Fig. 7). These are the nuclei which Löwe ('78) and Falchi ('87) found it so difficult to account for. From the beginning of the stage of differentiation

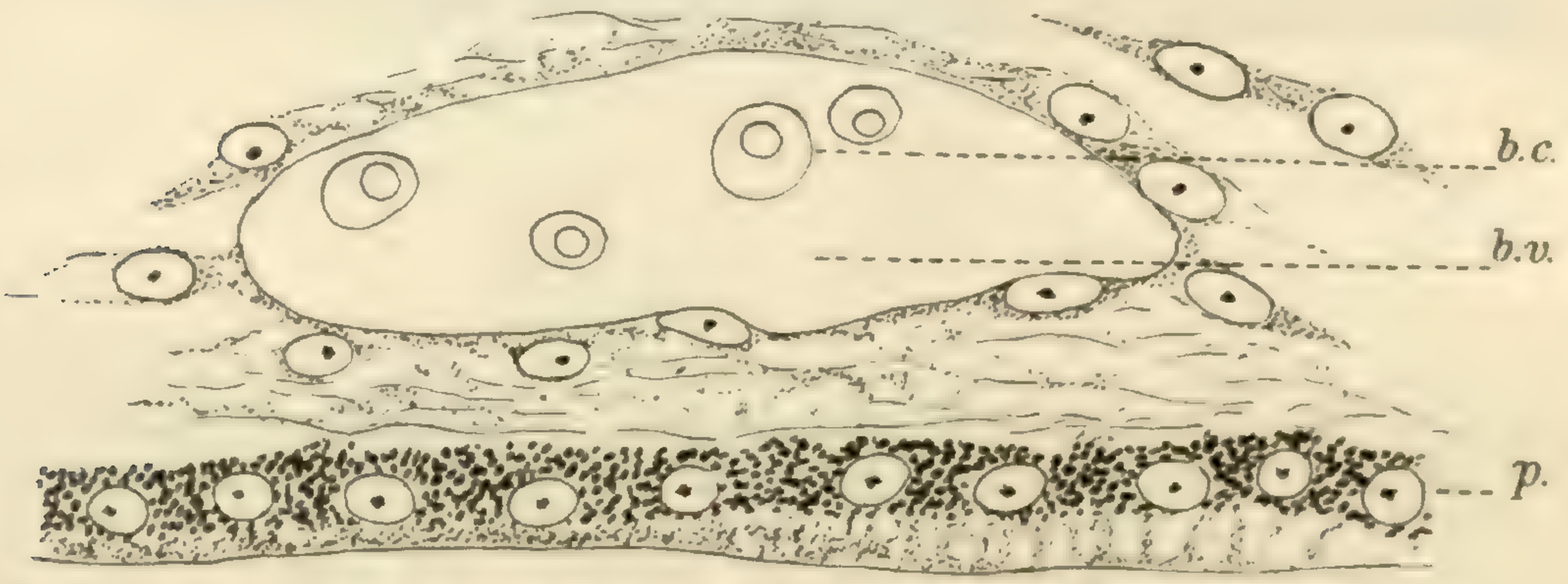

FIG. 10.— An 8½ days' embryo in which the pigment granules now fill the cytoplasm between the nuclei but do not yet occupy the cytoplasm between the external limiting membrane and these nuclei. x 810. *b. c.*, blood cell; *b. v.*, blood vessel; *p.*, pigment layer.

onwards there is a constant increase in width up to 44.2 μ which is the final thickness of the inner nuclear layer.

Up to the stage of completed development the structure of this layer is practically homogeneous throughout, but as differentiation proceeds, vacuoles appear next the ganglion-cell layer so that the appearance is like that in Fig. 15. Later the processes from the ganglion cells and the cytoplasmic strands from nuclei of the inner nuclear layer can be traced to varying depths, while the fibers of Müller extend perpendicularly across the layer from the internal limiting membrane to the membrane of Henle.

The outer reticular layer begins to develop four or five days later than the inner and toward the close of the period of cell multiplication. Viewed as a whole it presents in section the same crescentic appearance, but the horns of the crescent extend into

the undifferentiated region only half as far as those of the inner reticular layer (Fig. 4). Its width never increases but remains at 5.2 μ, though the boundaries are not so clearly defined at first and some straggling nuclei of the inner nuclear layer are still to be

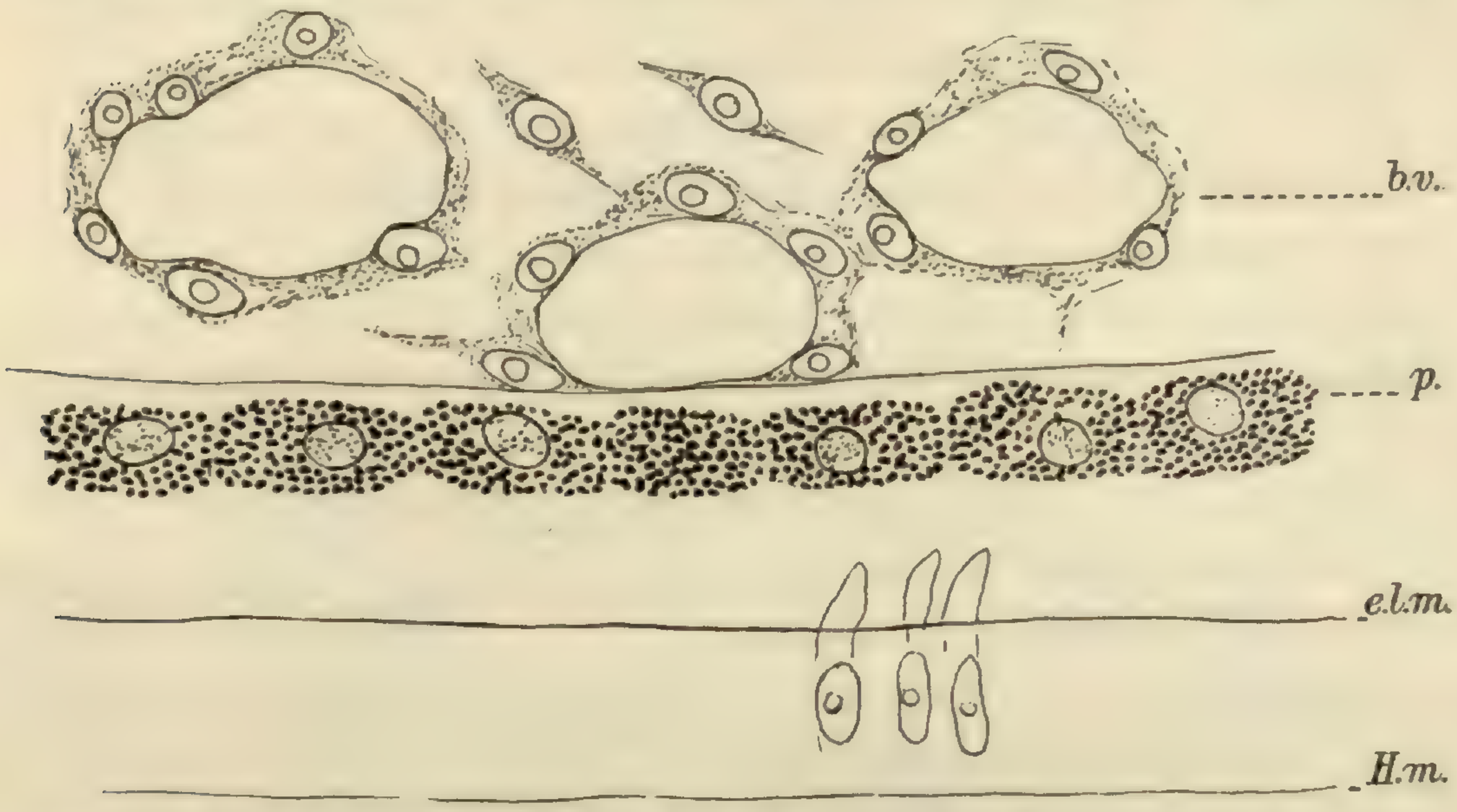

FIG. 11.— A 16½ days' embryo showing the cytoplasm of the pigment layer completely filled with pigment granules. x 810. *b. v.*, blood vessel; *e. l. m.*, external limiting membrane; *H. m.*, membrane of Henle; *p.*, pigment layer.

found in it up to the beginning of the stage of differentiation. At this stage the membrane of Henle is formed by the flattening of the inner ends of the rod and cone cells against the cytoplasm of the horizontal cells and against the ends of the fibers of Müller and of the processes from the inner nuclear layer (Fig. 13).

THE PIGMENT LAYER

The retina and the pigment layer, having as they do a common origin, develop in physical contact from margin to margin, and perhaps have an even more intimate connection, for the pigment layer probably plays an important *rôle* in the transfer of nutritive fluids to the multiplying nuclei and growing processes of the retina.

The pigment layer consists at first of two rows of closely packed nuclei, each 5.83 μ in diameter and surrounded by protoplasm which completely fills all the remaining space between the bounding membranes. The appearance is much like that suggested

by Fig. 3. It is a significant fact that even at this early stage there are always numerous large blood vessels in the choroid tissue just outside the pigment layer.

It will be noticed in Fig. 1 that growth of the pigment layer is

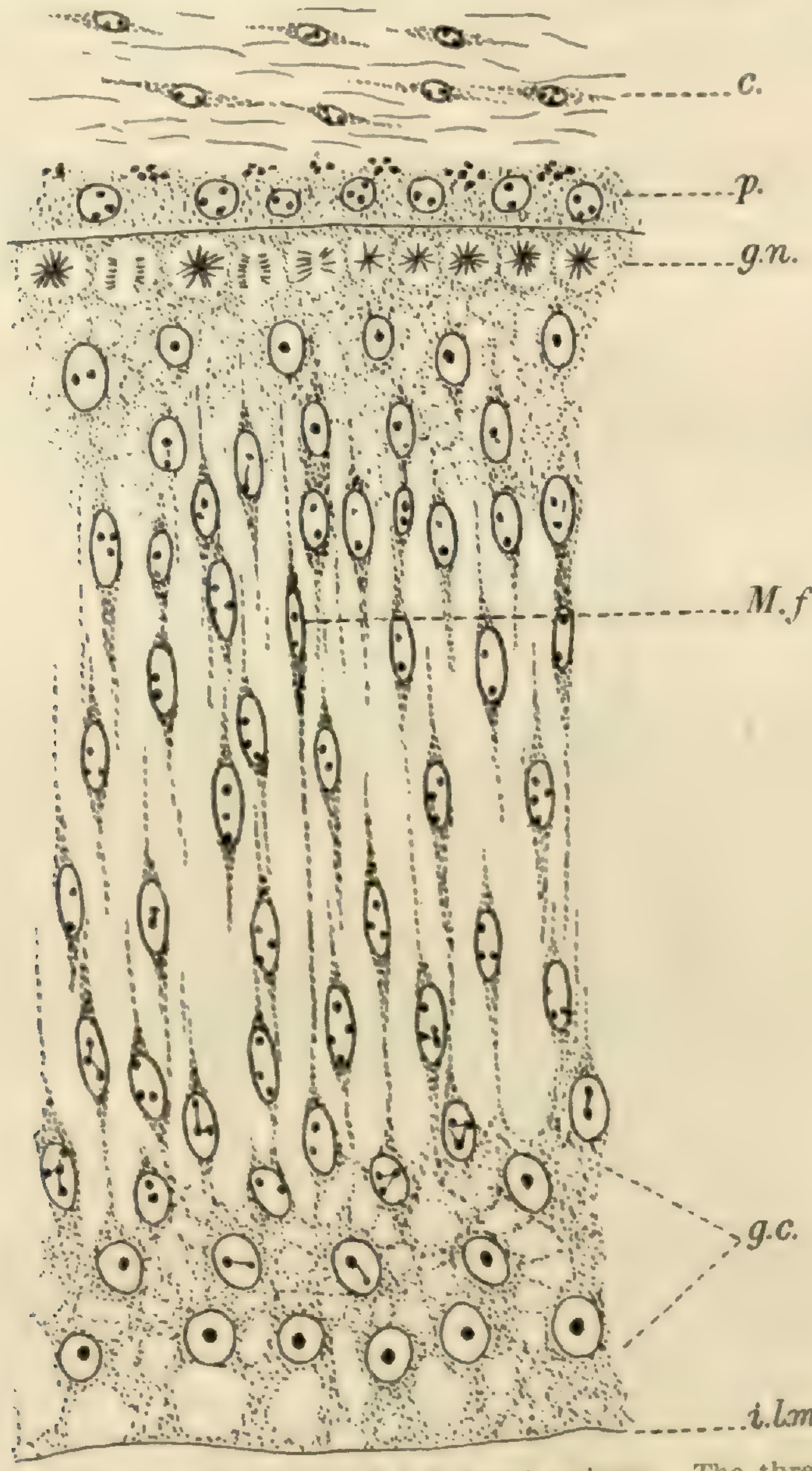

FIG. 12.—Section through the retina of a 7 days' embryo. The three layers of nuclei which will later become the ganglion-cell layer can be identified, as well as the bipolar cells of the inner nuclear layer, and the nucleus of a fiber of Müller is very distinct. Every nucleus of the germinal layer shows mitotic figures, the plane of division in each case being at right angles to the external limiting membrane; these nuclei are all imbedded in granular cytoplasm. x 810. *c.*, choroid; *g. c.*, ganglion-cell layer; *g. n.*, germinal nuclear layer; *i. l. m.*, inner limiting membrane; *m. f.*, radial fibers of Müller; *p.*, pigment layer.

at the margins and that even as early as two and two thirds days the surface area at the center of the cup has stretched out to such

an extent that the nuclei here have fallen into line so that the layer consists of a single row of nuclei. The condition at the margin of the optic cup remains the same as long as the eye continues to increase in size. Hence the row of actively dividing nuclei is always relatively short compared with that of the retina of which it is a direct continuation. After division the resulting

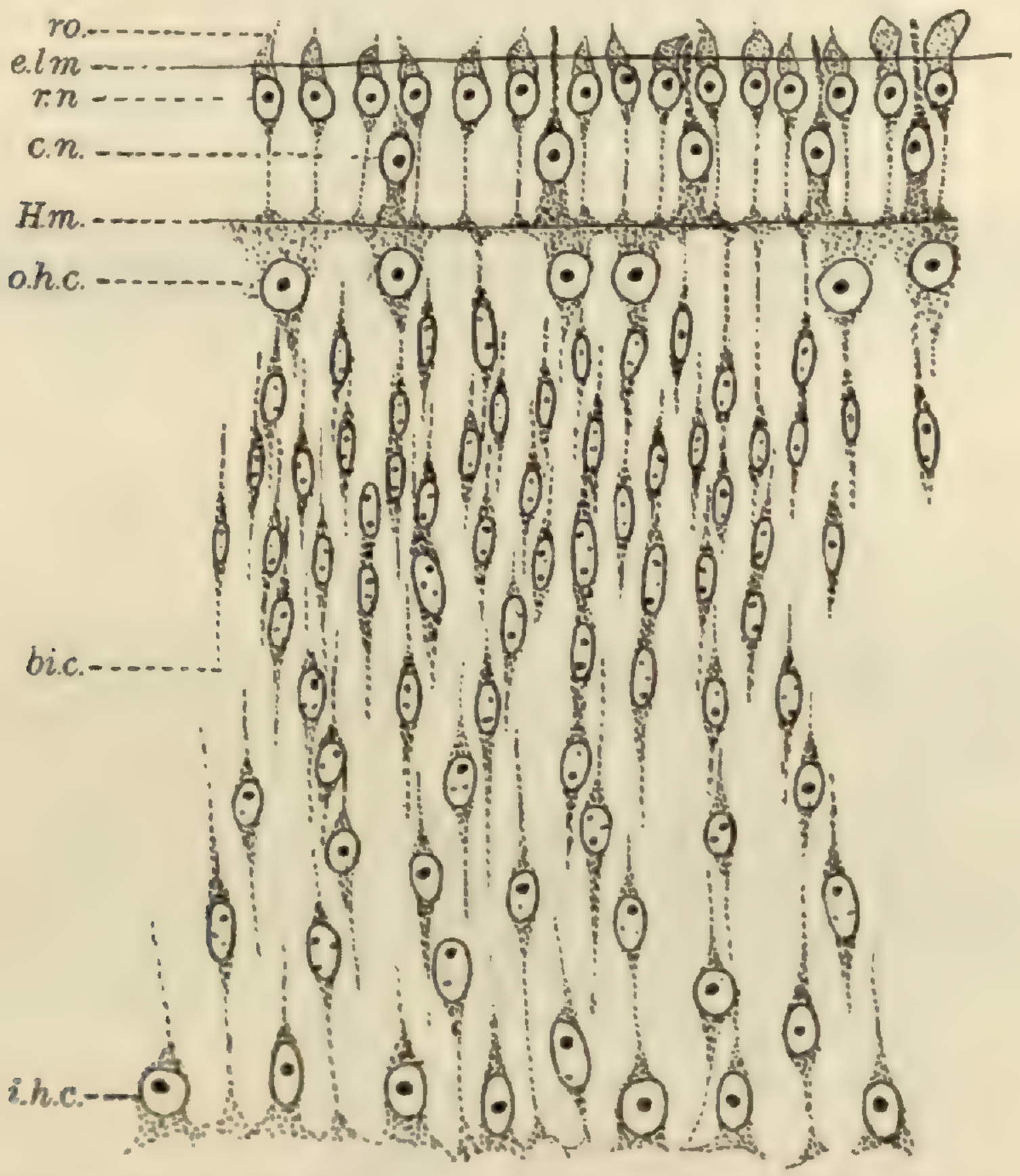

FIG. 13.— The retina of a 10½ days' embryo showing the structures outside of the inner reticular layer. In the inner nuclear layer can be distinguished the inner horizontal cells, the bipolar cells, the nuclei of the fibers of Müller and the outer horizontal cells. The outer reticular layer is forming, the membrane of Henle is distinct, and the outer nuclear layer shows the nuclei of the cones and of the rods in two layers. The cones appear as rather broad projections beyond the external limiting membrane and the cones as narrow cytoplasmic processes. x 810. *bi. c.*, bipolar cell; *c. n.*, cone nuclei; *e. l. m.*, external limiting membrane; *H. m.*, membrane of Henle; *i. h. c.*, inner horizontal cells; *o. h. c.*, outer horizontal cells; *ro.*, rods; *r. n.*, rod nuclei.

nuclei invariably grow to the size of the original nucleus, so there is never any apparent diminution in their size.

Pigment commences to form as early as three and two thirds days. Contrary to the statement which Cameron makes for the

frog, the granules begin to appear in the chick on the side of the layer away from the retina and in the protoplasm between the nuclei, which shows them to be of cytoplasmic origin (Figs. 8 and 12). Cameron says that in the frog they appear first on the side adjoining the retina. As development proceeds and the nuclei become farther apart these granules gradually fill all the cytoplasm of the pigment layer on the side farthest from the retina (Fig. 9). It will also be noticed that at the same time vacuoles

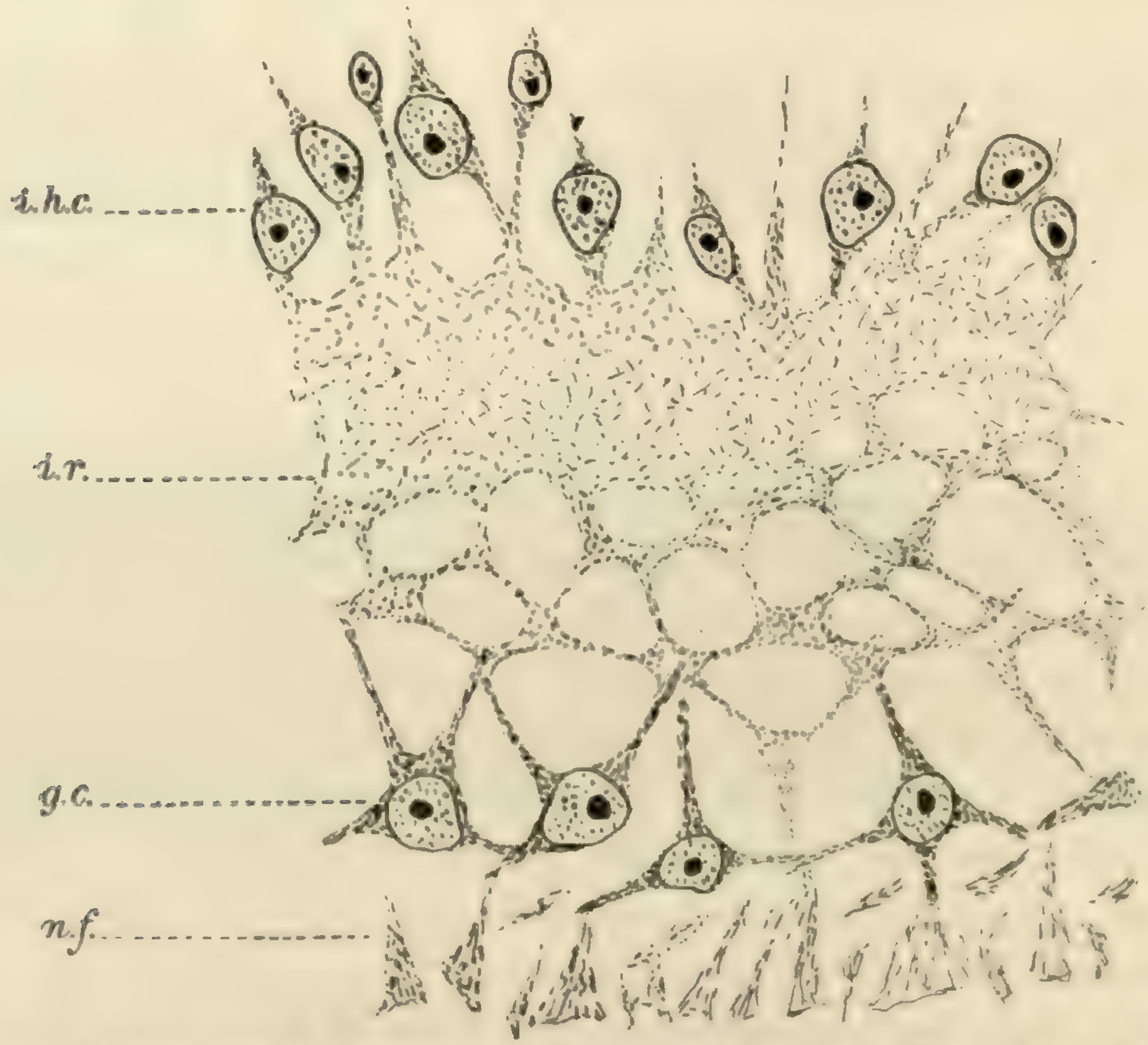

FIG. 14.— Inner portion of the retina of a 16½ days' embryo. The cells of the ganglion-cell layer now lie practically in a single plane. The inner reticular layer shows the large meshwork of its inner portion and the finer structure of its outer portion. x 810. *g. c.*, ganglion-cell layer; *i. h. c.*, inner horizontal cells; *i. r.*, inner reticular layer; *n. f.*, nerve-fiber layer.

begin to appear in the undifferentiated cytoplasm invariably present between the pigment layer and the external limiting membrane of the retina (Figs. 6 and 10). This cytoplasm is very minute in amount at an early stage of development and later increases greatly, taking the form of strands which are the beginnings of the future rods and cones and of the cytoplasmic streamers which finally develop from the pigment layer and extend inward

between them. Meanwhile the cytoplasm about the nuclei becomes differentiated to such an extent that by sixteen and one third days the layer is seen to be composed of clearly defined cells each completely filled with pigment granules (Fig. 11). Later all finer structure is entirely obliterated by the pigment, but no granules are ever found normally outside their enveloping cytoplasm. The significance of these facts in the development of the retina is seen in connection with certain theories which Bernard has elaborated. He believes that pigment is a nutritive substance which is constantly being ingested and absorbed by the growing retina. This theory had its origin in Miss Huie's article on Drosera, in which she has succeeded in establishing the fact of an intracellular digestion. Bernard goes so far as to describe streams of absorbed pigment stretching through the inner nuclear layer and forming the fibers of Müller. Cameron has accepted this theory and applied it in his study on the amphibian retina. The nuclei, he believes, put forth an unformed ferment or enzyme under the action of which the pigment granules are rendered available for the metabolism of the cell. In this way the rod and cone vesicles grow by successive digestions.

Before the theory is accepted, however, it must be shown that pigment is actually a food substance and not as generally supposed a waste product. The theory must be harmonized, too, with the fact that pigment granules are extremely resistant to the action of all known ferments or digesting fluids as Cameron himself states. A further objection to the theory lies in the fact that in the chick these granules first form on the side of the pigment layer away from the retina, so that the rods begin to develop before there is any pigment in their vicinity. If they are able to begin to grow without it, is it not at least possible that they might continue to develop without it? Further, pigment is never found outside the protoplasm of the pigment cell; none ever appears in the retina, or even in contact with the rods and cones during their development. Besides, may not the mediation of a third substance and in such an unavailable form be entirely superfluous, for cannot the rods and cones obtain nutritive material for their growth direct from the numerous blood vessels just outside the pigment layer?

The Outer Nuclear Layer

The outer nuclear layer, which forms during the period of readjustment, consists of two rows of nuclei. The one first laid down and adjoining the membrane of Henle is the layer of cone nuclei,

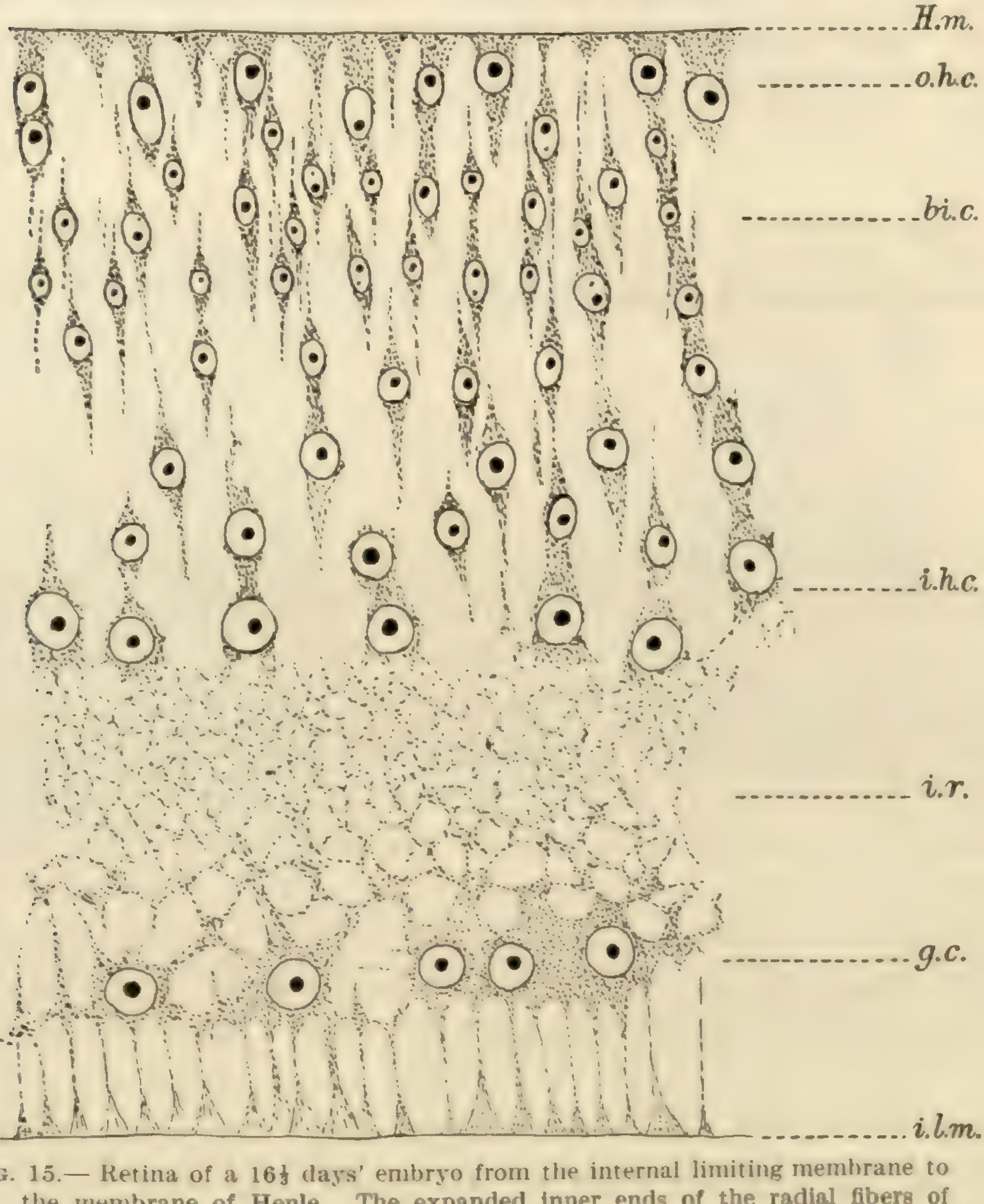

Fig. 15.— Retina of a 16½ days' embryo from the internal limiting membrane to the membrane of Henle. The expanded inner ends of the radial fibers of Müller are evident. The large nuclei of the inner and outer horizontal cells appear in the inner nuclear layer, the remaining nuclei in this layer belonging to bipolar cells and to the fibers of Müller. x 810. *bi. c.*, bipolar cell; *g. c.*, ganglion-cell layer; *H. m.*, membrane of Henle; *i. h. c.*, inner horizontal cells; *i. l. m.*, inner limiting membrane; *i. r.*, inner reticular layer; *o. h. c.*, outer horizontal cells.

which are fewer in number and more scattered in position (Fig. 13). The other, which borders on the external limiting membrane,

represents the last product of the division of the germinal nuclei. In fact, division among them does not wholly cease until the rods of their immediate neighbors have attained a high degree of development. Thus the rod nuclei are the youngest in the retina. All measure 4.38 μ in diameter, which is the regular size of the germinal nuclei after the first half of the first period of growth. They suffer no diminution in size with the development of the rods and cones, and least of all do they receive any accessions to their number by a migration of nuclei from the inner nuclear layer.

Long before division has ceased in the row of rod nuclei, in fact as soon as the outer nuclear layer begins to appear at the center of the retinal cup, the rudiments of the future rods and cones can be made out in the shape of cytoplasmic threads or strands between the pigment layer and the external limiting membrane. The rods and cones are clearly of cytoplasmic origin. This cytoplasm slowly increases in amount so that at the beginning of the stage of differentiation the appearance is like that shown in Fig. 13. It will be noticed that a fragment of the original protoplasmic thread still tips the ends of some of the rod rudiments, while the base of the rod appears drawn out into a finely attenuated stalk whose inner extremity flattens against the membrane of Henle. The base of the cone is shorter and much broader (Fig. 16). As development proceeds, little or no change takes place in the outer nuclear layer strictly so called except that the nuclei toward the close of the period of differentiation stain more deeply with the iron-alum hæmatoxylin. This is true of all retinal nuclei.

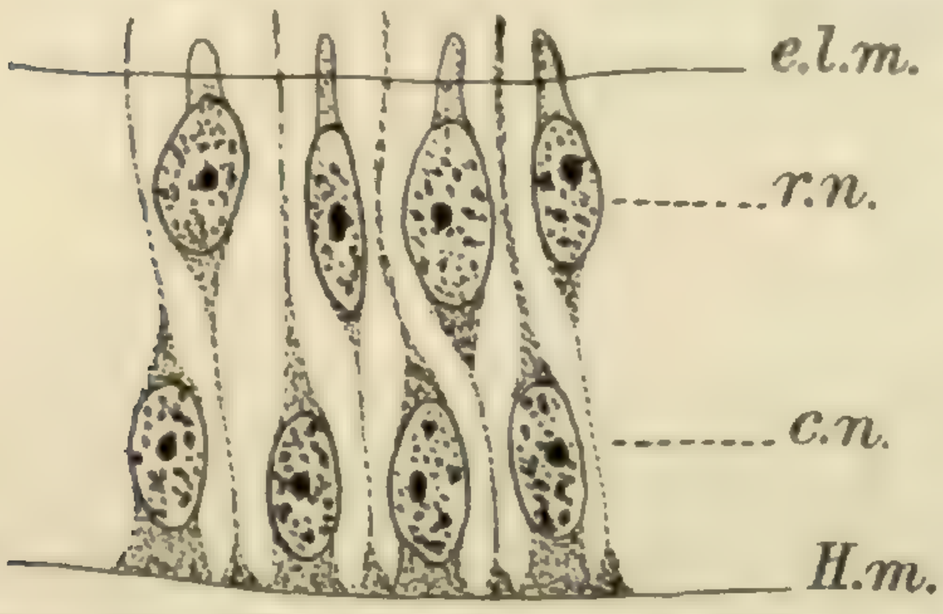

FIG. 16.— The development of the rods and cones in a 10 days' embryo. The rod-body is distinctly granular; the cone-body appears as a narrow cytoplasmic thread. x 1500. *c. n.*, cone nuclei; *e. l. m.*, external limiting membrane; *H. m.*, membrane of Henle; *r. n.*, rod nuclei.

The cytoplasm of the rods, which at first is evenly granular and homogeneous throughout, gradually increases in amount and assumes more and more the conical appearance presented in Fig. 17. About the middle of the period of differentiation, a clear

unstaining vesicle appears at the tip or outer segment and persists in the same size and shape during the remainder of the development of the rod. There is no evidence that it is of nuclear origin in the chick, although Cameron describes it as such in the frog. The cytoplasm between this vesicle and the rod nucleus gradually elongates as development proceeds but without any appreciable increase in amount since at the same time the diameter diminishes, and eventually a conical cap of protoplasm develops on the distal end so that the unstaining vesicle appears like a fluid-filled vacuole imbedded in the rod about a fourth the way from the finely tapering point.

An interesting statement in this connection is made by Bernard, and repeated in more elaborate form by Cameron, to the effect that the nuclei of the rods tend to become protruded to varying degrees beyond the external limiting membrane. This certainly does not seem to be the case in the chick, although at first glance the appearance is strikingly in accord with such a statement. In the base of many of the rods and just outside the external limiting membrane appears a structure that might easily pass for a nucleus. The object proved a puzzle for a time, but with more careful study its explanation became clear. It was found that all the rods do not stand exactly perpendicular to the external limiting membrane, but many of them are bent over at various angles with it; and consequently these structures that look so much like nuclei are the truncated ends of other rods that once pointed toward the observer. By

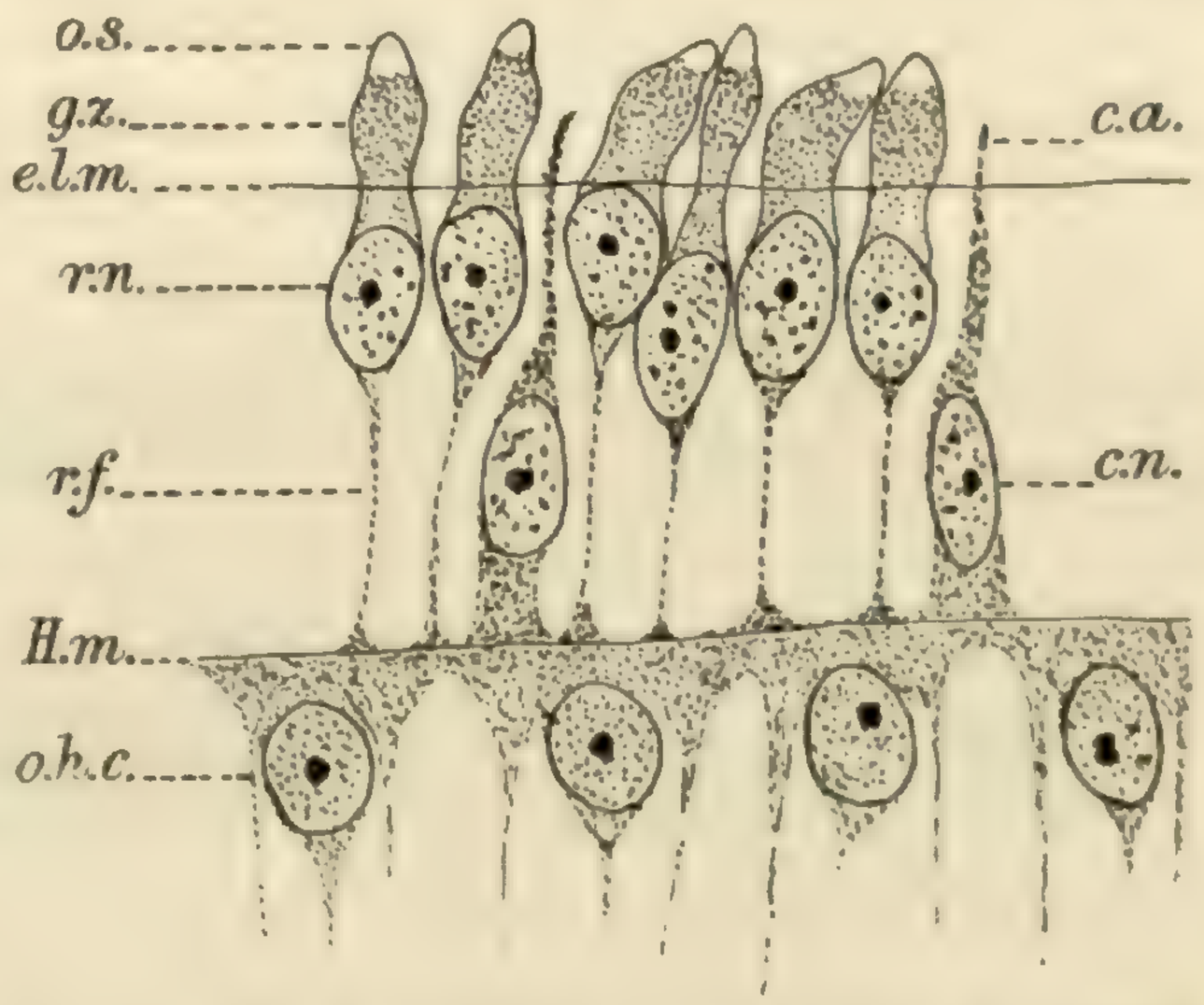

FIG. 17.— The developing rods and cones in an 11 days' embryo. The rods now show a clear outer segment and a granular inner zone. The cones are essentially the same as in the preceding figure. x 1500. *c. a.*, cone anlage; *c. n.*, cone nuclei; *e. l. m.*, external limiting membrane; *g. z.*, granular zone of rod; *H. m.*, membrane of Henle; *o. h. c.*, outer horizontal cells; *o. s.*, outer segment of rod; *r. f.*, rod fiber; *r. n.*, rod nuclei.

focusing down on them the remainder of the stump can be traced to its own nucleus. Hence the rod nucleus invariably retains its early position wholly inside the external limiting membrane. We have been unable to find such effects in the chick as Cameron figures in the frog in his Pl. 51, Figs. 24 and 29, where the nucleus forms a distinct projection beyond the limiting membrane.

VARIATIONS IN THE RELATIVE RATE OF DEVELOPMENT

In the development of the retina the time of appearance of the different elements is not absolutely fixed. An eye at ten days may have reached the same degree of development as another at twelve, or again it may be no further advanced than some that are two days younger. In the same retina it might be expected that the state of development of one layer would bear some definite relation to that of the others. But this is not the case. When the ganglion-cell layer has reached the stage shown in Fig. 6, the inner nuclear layer may appear as shown in that figure, or it may be more or less highly developed. Very frequently the inner nuclear layer reaches a very advanced stage before any cytoplasmic changes in the outer nuclear layer have begun to appear at all. On the other hand the rods and cones may be developing rapidly while the other layers are still in the earlier stages. The fact has been mentioned before that when the majority of the rods are in an advanced stage of development others are found beside them whose nuclei have just ceased dividing and whose rudiments have not begun to develop at all. Hence from the appearance of a part it is impossible to predict the stage of development of any other, for there appears to be no definite developmental ratio that might serve as a criterion. The drawings in each case are from the more typical representatives, and give the appearance most frequent at the specified age.

SUMMARY AND CONCLUSIONS

1. The retina consists at first of a syncytium.

2. Most of these nuclei eventually go to form the ganglion-cell layer; those next the external limiting membrane become the germinal nuclei.

3. Only the row of germinal nuclei has the power of division.

4. There are three well defined periods of growth: (*a*) the period of cell multiplication, second to eighth day; (*b*) the period of readjustment, eighth to tenth day; (*c*) the period of final differentiation, tenth day to end of incubation.

5. Up to the end of the first period the retina grows from within outward by the deposition of an additional row of nuclei with each successive generation.

6. After this, karyokinetic figures are found only at the margins.

7. Differentiation begins at the center of the retinal cup and gradually spreads in every direction toward the growing margins.

8. Between the center of the optic cup and the growing margin of any given retina are represented all the different stages through which it has passed; the nearer the margin, the younger the stage.

9. The ganglion-cell layer consists at first of three rows of nuclei.

10. These fall into line in the direction of the internal limiting membrane so as eventually to form but one layer.

11. In the inner nuclear layer differentiation into horizontal cells, fibers of Müller, and bipolar cells takes place *pari passu* with the formation of these nuclei.

12. This layer consists at first of about fourteen generations of nuclei.

13. With the exception of the horizontal cells each successive generation fails to attain quite the size of the one preceding.

14. As development proceeds the number of rows of nuclei decreases from fourteen to eight by a closing up of the ranks in the direction of the external limiting membrane.

15. Up to the end of the period of readjustment the nuclei of this layer are elliptical in outline with the long axis at right angles to the external limiting membrane.

16. Later these nuclei become circular in outline.

17. The reticular layers are cytoplasmic in both origin and structure.

18. The pigment layer is a direct continuation of the retina.

19. Like the retina its early structure is also a syncytium.

20. The nuclei at first are in two rows which early become arranged as one with the stretching out of the surface area.

21. Active growth is restricted to the margins of the pigment layers and continues as long as the eye increases in size.

22. Nuclei of this layer are always of the same size as those found in the early undifferentiated condition.

23. Pigment granules first form on the side of the layer away from the retina and in the protoplasm between the nuclei.

24. These granules are never normally found outside the cytoplasm of the pigment cell.

25. There is no evidence that pigment is a food substance.

26. The numerous large blood vessels always present in the choroid coat next the pigment layer may furnish the nutritive material for the development of the retina.

27. The outer nuclear layer represents the last two generations from the division of the germinal nuclei.

28. The rod nuclei are the youngest in the retina.

29. They are more numerous than the cone nuclei, and division among them does not wholly cease until the rods of their immediate neighbors have attained a high degree of development.

30. The rods and cones have their origin in undifferentiated cytoplasm.

31. There is no evidence that any part of the rod or cone is of nuclear origin.

32. The nuclei of the rods and cones retain their early position wholly within the external limiting membrane and do not tend to become protruded to varying degrees beyond it, as has been recorded for other animals.

33. In the development of the retina there is no fixed time for the appearance of the different elements.

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NOTES ON MARINE COPEPODA OF RHODE ISLAND

LEONARD WORCESTER WILLIAMS

Work upon the non-parasitic Copepoda of America is very fragmentary. In recent years the papers of Wheeler, of Giesbrecht, and of Herdman, Thompson, and Scott record a relatively small number of forms from what is apparently an extremely rich fauna. Miss Rathbun's check-list of the Crustacea of New England records twelve free-swimming marine Copepoda. None of these, however, is reported in the waters of Rhode Island.

This list records twenty-six free-swimming Copepoda, one parasitic form, and a metanauplius of a parasitic copepod. Of the free-swimming Copepoda eleven have been reported previously: eight by Herdman, Thompson, and Scott from the Gulf of St. Lawrence and six by Wheeler from the Wood's Hole region. We also describe three new species.

The material upon which this paper is based was obtained in Narragansett Bay. Winter collections were made above Rocky Point and summer collections near Wickford, and in Charlestown Pond during the entire summer. The latter is situated in southern Rhode Island and is a large shallow inlet (six miles long by one broad) from the Atlantic. It is slightly brackish but the copepod fauna is much the same as that of the bay.

I am indebted to Dr. A. D. Mead of Brown University for the use of preserved material collected at Wickford by the Rhode Island Commission of Inland Fisheries; to Professor C. B. Wilson for kind assistance; and to Mr. Samuel Henshaw for the use of books from the Museum of Comparative Zoölogy at Harvard.

Type specimens of the new species have been deposited in the museum of the Boston Society of Natural History.

Calanus finmarchicus (Gunnerus)

1765. *Monoculus finmarchicus* Gunnerus.
1863. *Cetochilus helgolandicus* Claus.

1864. *Calanus finmarchicus* Boeck.
1878. *Calanus finmarchicus* Brady.
1892. *Calanus finmarchicus* Giesbrecht.
1903. *Calanus finmarchicus* Sars.

This is a species widely distributed in the North Atlantic and Arctic Oceans, having been taken by Nansen's expedition above 85° north latitude. It has been twice reported from American waters, by Thompson and Scott ('98) and by Wheeler (:00). It appeared abundantly in tows taken in Narragansett Bay in January but was found at no other time. The specimens agree with those taken by Wheeler in lacking the marked concavity of the inner border of the basal joint of the fifth pair of legs of the female.

Pseudocalanus elongatus (Boeck)

1864. *Clausia elongata* Boeck.
1878. *Pseudocalanus elongatus* Brady.
1892. *Pseudocalanus elongatus* Giesbrecht.
1898. *Pseudocalanus elongatus* Thompson and Scott.
1903. *Pseudocalanus elongatus* Sars.

Narragansett Bay, January, February. This is a decidedly northern form, its southern European limit being the northern coast of France.

Centropages hamatus (Lilljeborg)

1853. *Ichthyophorba hamata* Lilljeborg.
1863. *Ichthyophorba angustata* Claus.
1864. *Centropages hamatus* Boeck.
1892. *Centropages hamatus* Giesbrecht
1898. *Centropages hamatus* Thompson and Scott.
1900. *Centropages hamatus* Wheeler.
1903. *Centropages hamatus* Sars.

Narragansett Bay, January, February. Wickford, summer.

PSEUDODIAPTOMUS Herrick

1884. *Pseudodiaptomus* C. L. Herrick.
1890. *Schmackeria* Poppe and J. Richard.
1894. *Heterocalanus* T. Scott.
1894. *Weismannella* Dahl.

Head separated from, or fused with the first thoracic segment; fourth and fifth segments of the thorax fused (or not). Abdomen of the female 4- or 3-jointed. Furca at least two and a half times as long as broad, with six setæ. First antenna 20- to 22-jointed. Terminal section of the grasping antenna of the male usually 2-jointed. The second antenna with a long outer ramus of two to four joints. Outer ramus of mandible 3- or 4-jointed; inner ramus inconspicuously 2-jointed, its second joint curved outward strongly. The first joint of the basipodite of the second maxilla is divided into two sections. Basipodite of the maxilliped short and strong, inner ramus 4- or 5-jointed, some of its bristles branched. The inner and outer rami of the first to fourth leg 3-jointed, terminal joint of the outer ramus with two outer spines and a terminal spine serrated externally. The inner ramus of the fifth limb of the female rudimentary or absent, outer branch 2- or 3-jointed. Inner ramus of the left fifth limb of male usually rudimentary, rarely absent or transformed into a grasping organ; outer ramus 2-jointed, occasionally reduced to a claw-shaped process of the basipodite. Inner ramus of the right fifth limb rudimentary or lacking; outer ramus 2- or 3-jointed with an end claw. One or two egg sacs.

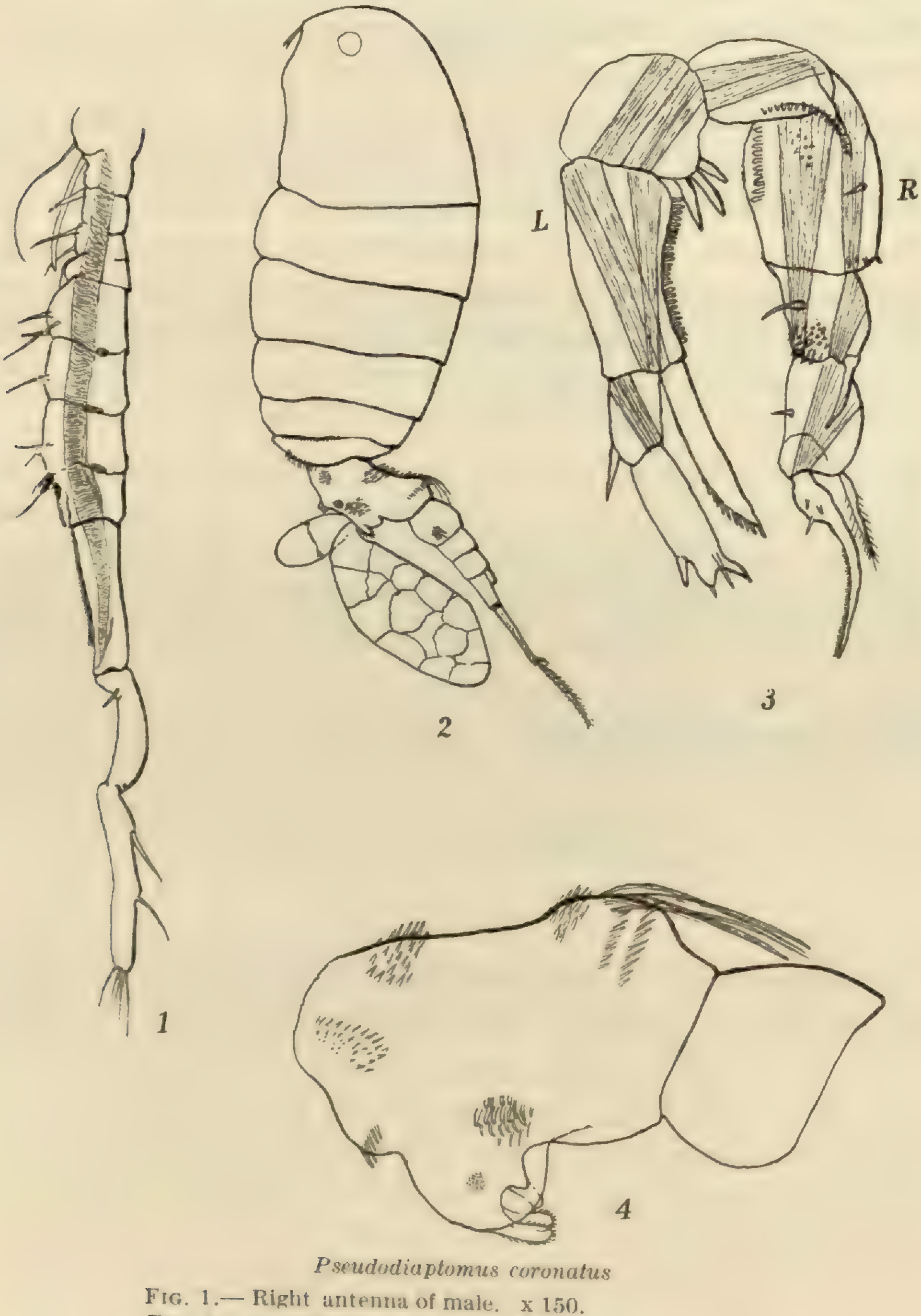
Pseudodiaptomus coronatus n. sp.

Figs. 1–7

The generic description must be modified slightly to admit this species: the fourth and fifth thoracic segments are not fused and the seventh and eighth segments of the first antenna are not completely fused and if they are considered separate the first antenna is 23-jointed. In other respects the species agrees with the generic description. The last thoracic segment (Fig. 2) is rounded posteriorly and is naked in the male and haired in the female. The fourth thoracic segment is spined in the female and naked in the male. Abdomen of male 5-jointed; of female 4-jointed. Almost all bristles of the feet and furca are jointed some distance from their bases (Fig. 7).

Female.— First segment of abdomen much swollen with spines

and bristles arranged asymmetrically, and with a pair of spatulate flaps (Figs. 4 and 5) extending over the genital aperture. The bristles of the left side of the genital segment in both areas are

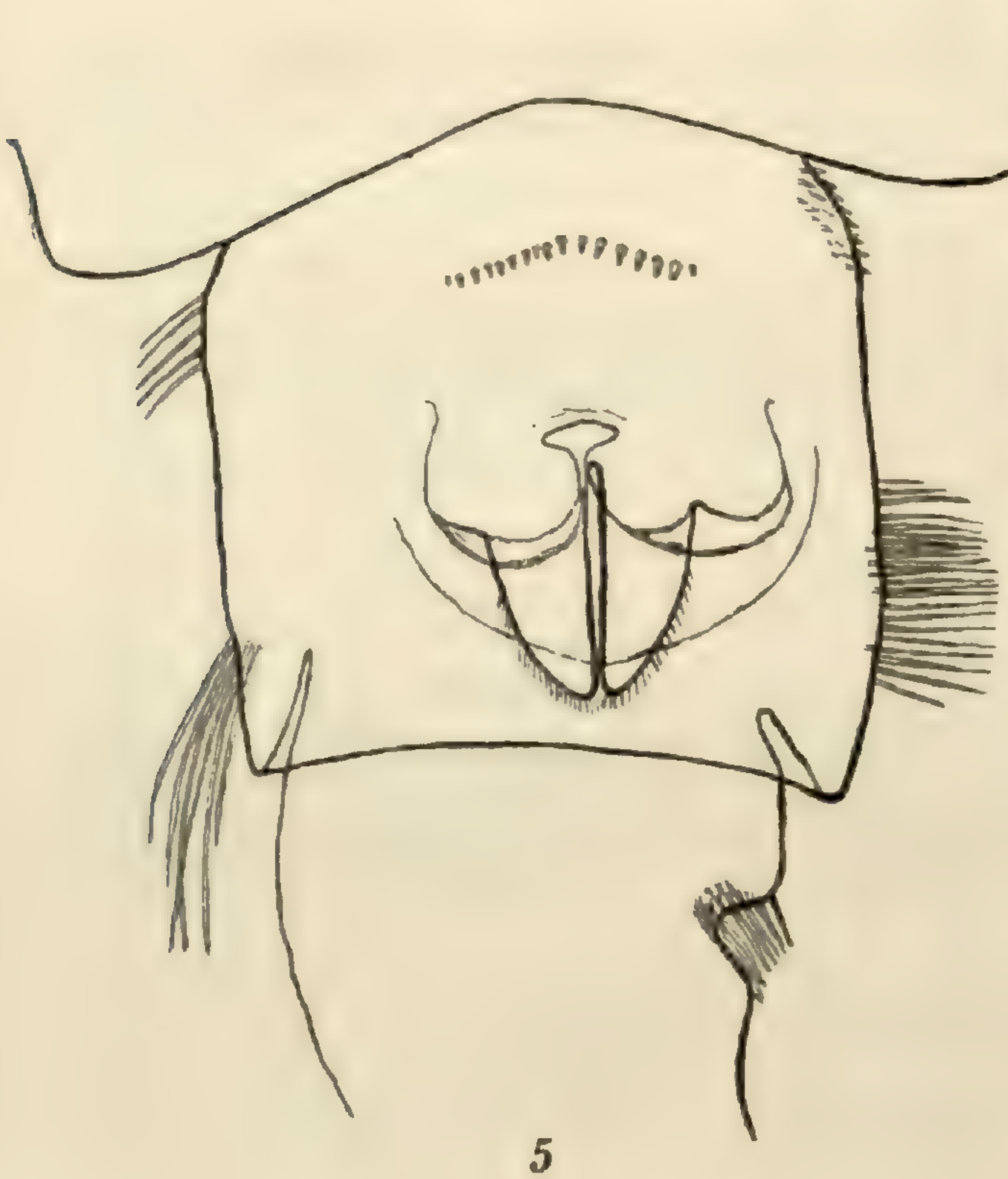


Pseudodiaptomus coronatus

FIG. 1.— Right antenna of male. x 150.
FIG. 2.— Lateral view of female. x 50.
FIG. 3.— Fifth limbs of male, posterior surface. x 130.
FIG. 4.— Left side of the genital segment of female. x 175.

respectively much longer than those of the right side. A small tuft of very long soft bristles near the posterior edge of the dorsal

surface projects almost across the second segment. The left side of the second segment of the abdomen has a small depression filled with heavy bristles while the right side is convex and bears a few spines (below the middle and so not shown in the drawing). The last segment has a crown of spines, on the posterior edge. The furca is slightly asymmetrical and each ramus is five times as long



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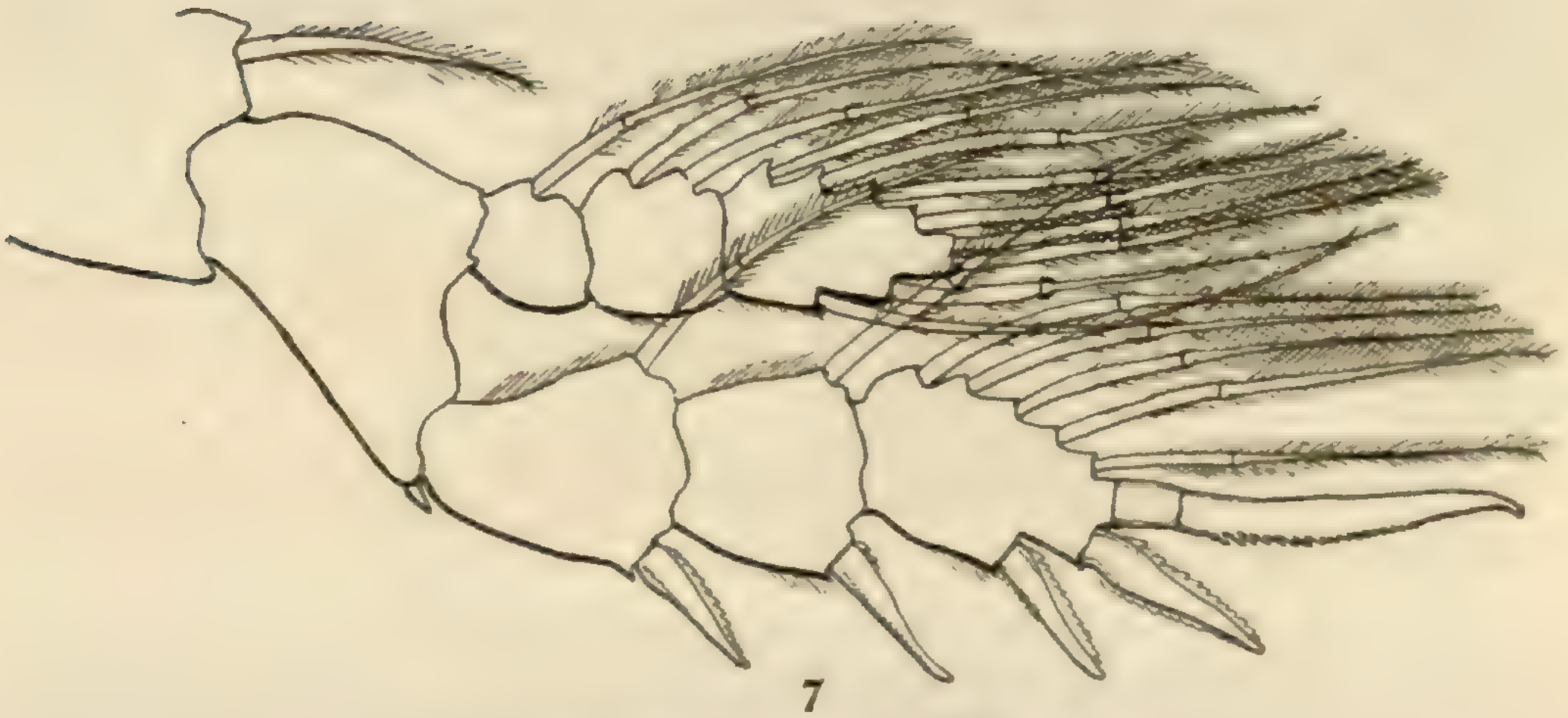

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Pseudodiaptomus coronatus

FIG. 5.— Genital segment of female, ventral surface. x 175.
FIG. 6.— Fifth limbs of female, posterior surface. x 175.
FIG. 7.— Third swimming foot, female. x 280.

as broad and has long delicate bristles on the inner edge and shorter and stronger bristles on the outer edge. The fifth limbs are alike (Fig. 6) and 4-jointed. The terminal joint is prolonged at the inner angle into a toothed lamella and has a spine at the outer angle. The terminal claw is toothed along its inner (concave) border and has a naked lamella on the inner side at base. One large and one (right) small egg case.

Male.— Abdomen long and slender. First joint bristled along the upper part of its posterior edge and with a semicircle of bristles on the lower surface. The upper part of the hinder edge of the second joint and the entire posterior edge of the third, fourth, and fifth joints have a crown of triangular spikes. The furca is three times as long as broad and lacks marginal bristles. The right fifth limb (Fig. 3) has no inner ramus; outer ramus 2-jointed with a terminal claw. First joint of basipodite has a slender curved process coarsely toothed along its inner edge, the second joint and the first joint of the outer ramus are toothed inside. The second joint of the inner ramus has a bristled spine and a curved terminal claw toothed on the inner edge and swollen at base. The left fifth limb biramous. The first joint of the basipodite has a cluster of three or four broad radiating spines. The second joint has coarse teeth on its inner edge. The inner ramus is a blade toothed along the distal half of its curved outer edge. The outer ramus is 2-jointed; the first joint has an outer terminal spine and the second joint ends irregularly in four spines. The right antenna (Fig. 1) has a terminal section of two joints and has the third joint from the end toothed along its anterior edge.

Length of female 1.5 mm.; of male 1.2 mm.

Narragansett Bay and Charlestown Pond.

Temora longicornis (O. F. Müller)

1785. *Cyclops longicornis* Müller.
1850. *Temora finmarchica* Baird.
1865. *Temora longicornis* Boeck.
1878. *Temora longicornis* Brady.
1892. *Temora longicornis* Giesbrecht.
1898. *Temora longicornis* Thompson and Scott.
1900. *Temora longicornis* Wheeler.
1903. *Temora longicornis* Sars.

Narragansett Bay, January, February.

Eurytemora Giesbrecht

1881. *Eurytemora* Giesbrecht.
1881. *Temorella* Claus.

Body moderately slender, rostrum with small, soft lappets. Fifth thoracic segment free, often expanded laterally. Abdomen slender, genital segment slightly protruding downward. Furca elongated, symmetrical. Anterior antenna in female comparatively short, scarcely longer than the cephalothorax, 24-jointed. Right antenna of male geniculate, terminal portion of two (three?) joints. Posterior antenna with outer ramus longer than inner and 7-jointed. Mouthparts similar to those of Temora except that the posterior maxillipeds are shorter and stouter. Inner ramus of the first leg 1-jointed, of the second to the fourth, 2-jointed. Fifth legs of female 4-jointed, penultimate joint produced on the inside into a strong, pointed process; terminal joint small. Fifth legs of male 4- or 5-jointed, about equal; terminal joint of right leg claw-shaped, of left, spatulate or dilated.

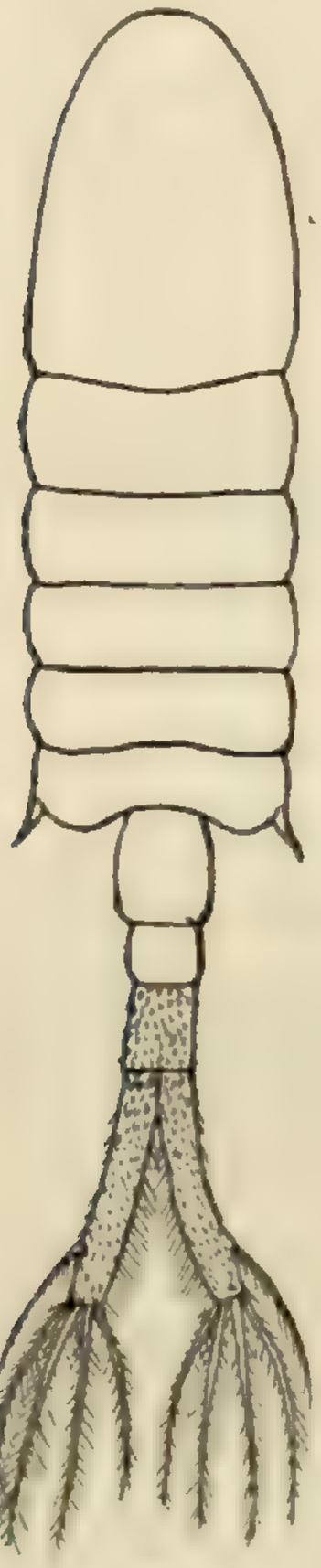
Marine, brackish, and fresh water.

Eurytemora americana n. sp.

Figs. 8–11

Female.—The lateral angles of the last segment of the thorax (Figs. 8 and 10) are drawn out into conspicuous triangular wings which are distinct from the rounded posterior surfaces of the segment. The wing arises from the lower two thirds of the outer side of the segment and its upper edge is slightly concave, and its lower edge slightly convex. In lateral view it forms, with the hinder edge of the segment, an S-shaped outline. The abdomen is 3-jointed; the genital segment is evenly rounded at the sides and above but projects below; the genital opening is covered by a broad, cordate flap. The upper surface of the anal segment and furca is covered with short, strong spines. The furcal arm is eight times as long as broad, curved outward a little, and slightly tapering. The furcal setæ, except the dorsal ones, are as long as the furca, coarse, and swollen at the base. The dorsal seta is short and

jointed near the base. First antenna as long as the trunk and strong. The fifth limb (Fig. 11) is similar to that of *E. lacustris* but the penultimate joint is longer, and its inner process is more slender and is finely bristled on both edges. The terminal joint



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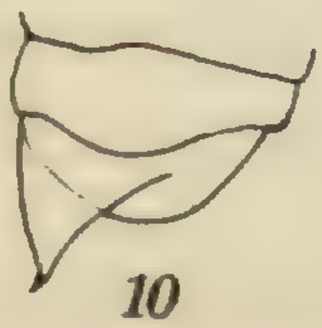

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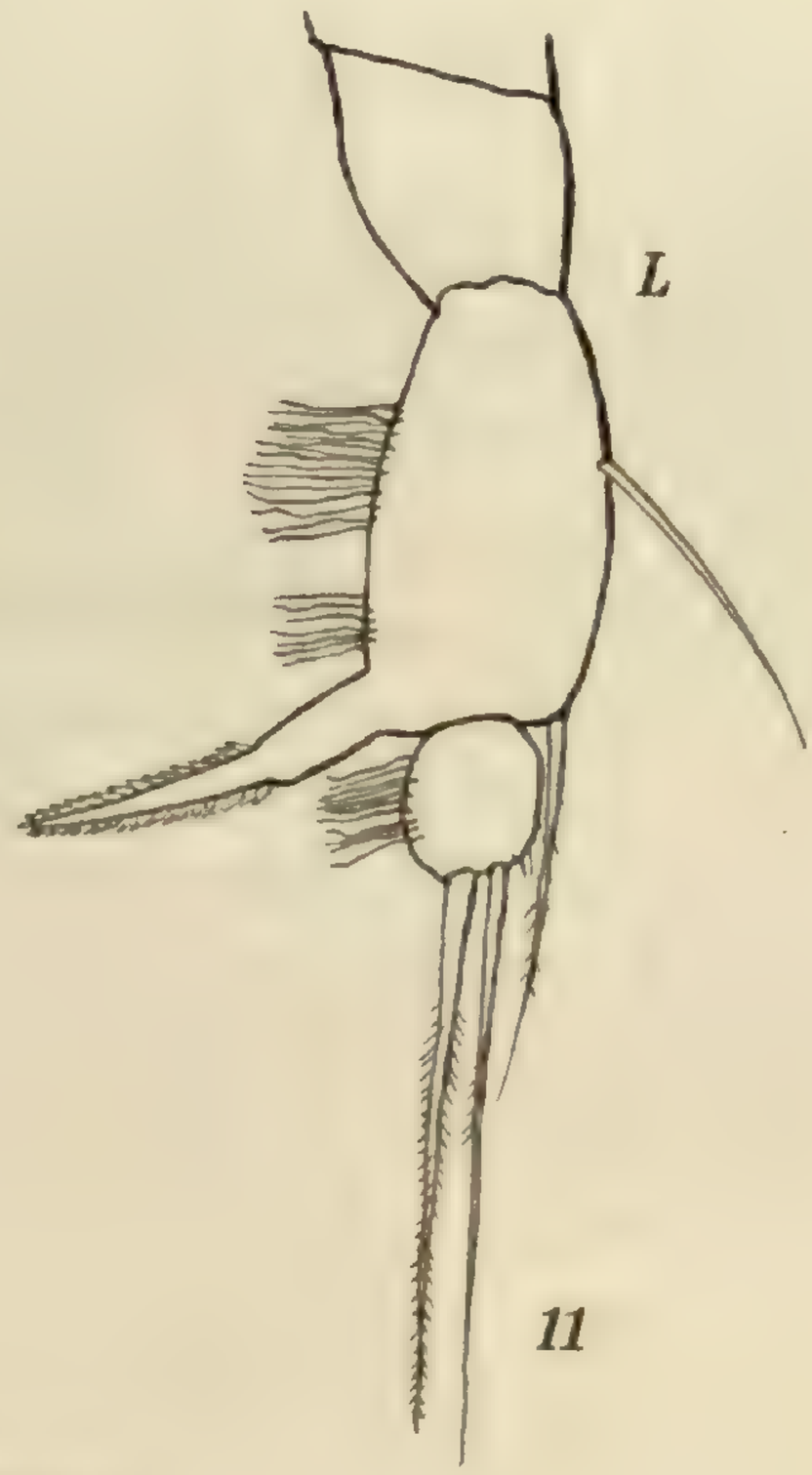

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Eurytemora americana

Fig. 8.— Dorsal view of female. x 40.
Fig. 9.— Fifth limbs of male, anterior surface. x 350.
Fig. 10.— Left side of the fourth and fifth segments of female.
Fig. 11.— Left fifth limb of female, anterior surface. x 350.

bears two setæ of nearly equal length, but the inner one is heavier and is more distinctly bristled. The inner edges of the last and next to the last joints bear long, slender bristles. Eggs light green.

Male.— Lateral angles of the last thoracic segment rounded.

Abdomen slender, 5-jointed. Anal segment with few spines and furca without spines on the upper surface. Furca six times as long as broad, inner edge with long slender bristles. Furcal setæ as in the female, therefore longer than the furca. The left first antenna is relatively longer than in the female, reaching to the second segment of the abdomen. Right first antenna as in *E. herdmani*, *i. e.*, about as long as left antenna, very heavy, and with the terminal portion composed of two long segments and a minute terminal segment; seventeenth and eighteenth joints with a comb-like ridge; nineteenth joint with a notch on the anterior side at base and two toothed ridges beyond the notch. The right fifth limb (Fig. 9) is 5-jointed, the last two not being fused and the next to the last slightly swollen at base. Left fifth limb 5-jointed, the last joint separated from the fourth joint by an oblique hinge and ending in three lobes, each with a spine upon its apex.

The first to fourth limbs of both sexes are very similar to those of *E. velox*.

Length of ♀, 1.8 mm.; cephalothorax, 1.07 mm.

Length of ♂, 0.9 mm.; cephalothorax, 0.68 mm.

Narragansett Bay, January to April; Charlestown Pond, summer.

Males and females of this species were brought through the last molt to sexual maturity. The males happened to molt earlier than the females, and for some days each carried a spermatophore by its stalk in the fifth limb, another spermatophore being almost or quite fully formed within the body.

Eurytemora hirunoides (Nordquist)

1888. *Temorella affinis* var. *hirunoides* Nordquist.
1898. *Eurytemora affinis* var. *hirunoides* Giesbrecht and Schmeil.
1903. *Eurytemora hiruno des* Sars.

Narragansett Bay, January; Charlestown Pond, July.

The specimens agree very closely with Sars' description and plates of the Norwegian form.

Eurytemora herdmani Thompson and Scott

1898. *Eurytemora herdmani* Thompson and Scott.
1898. *Eurytemora herdmani* Giesbrecht and Schmeil.

Narragansett Bay at Wickford. This species has been reported previously from the Gulf of St. Lawrence only.

Acartia tonsa Dana

1849. *Acartia tonsa* Dana.
1892. *Acartia tonsa* Giesbrecht.
1900. *Acartia tonsa* Wheeler.

Charlestown Pond. Abundant throughout the summer. The predominant copepod in the tow. The fifth limbs of the female are symmetrical in all the specimens examined and not as in Wheeler's figure.

Acartia clausii Giesbrecht

1892. *Acartia clausii* Giesbrecht.
1895. *Acartia clausii* Thompson.
1898. *Acartia clausii* Thompson and Scott.
1903. *Acartia clausi* Sars.

Narragansett Bay. Abundant in January and February. This species has a very wide distribution, occurring in the Atlantic, Mediterranean, the Black Sea, and the Gulf of Guinea (Scott, '94). Thompson and Scott found it in the Gulf of St. Lawrence but this is the first report of its occurrence in New England waters.

TORTANUS Giesbrecht

1883. *Corynura* Brady.
1892. *Corynura* Giesbrecht.
1898. *Tortanus* Giesbrecht and Schmeil.

Head without lateral hooks; eye large, without cuticular lens; no rostrum; a horseshoe-shaped fringed lamella in front of the upper lip. Thorax symmetrical, last segment separate or fused with the preceding. Abdomen of female often laterally compressed, 2- or 3-jointed. First antenna like that of Acartia, but the middle section of the gripping antenna is thicker. Two rami of the second antenna of nearly equal length; terminal segment of outer ramus rudimentary. Two rami of the mandible inserted at the end of the elongated second joint of the basipodite. First maxilla consisting of the first joint of the basipodite and the two much bristled

inner border lobes. Proximal lobes of the second maxilla much reduced. Maxillipeds 3-jointed. Inner ramus of first to fourth swimming feet 2-jointed (or the first with 3 joints). Fifth limb with one ramus in female, 2- or 3-jointed in the male, similar to Acartia, but stronger.

Tortanus setacaudatus n. sp.

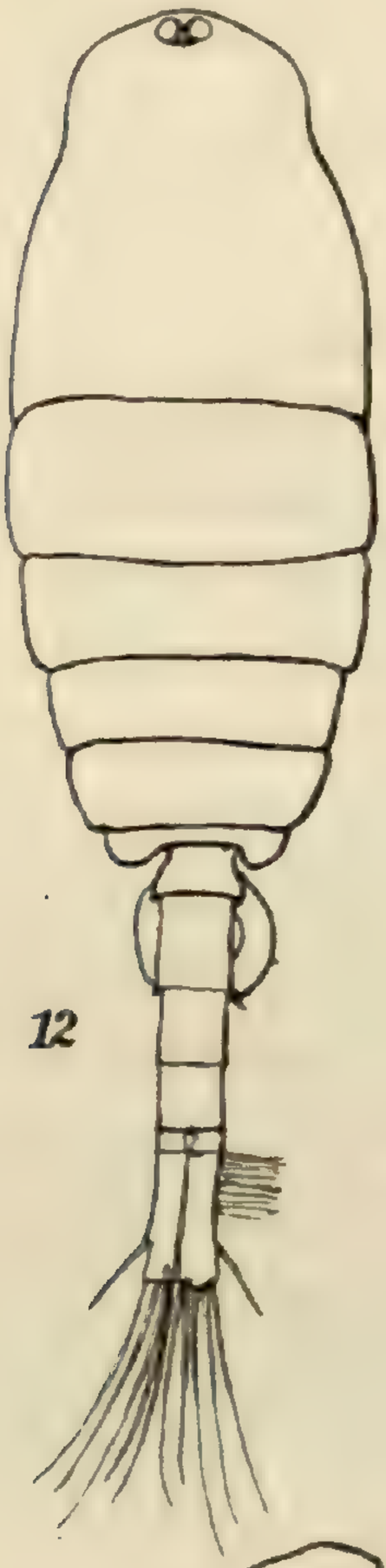
Figs. 12–15

Last thoracic segment free. First antenna long, 17-jointed, reaching beyond the end of the furca by one or two joints. The maxillipeds are extraordinarily large and are carried in a very characteristic manner, *i. e.*, horizontally and at right angles to the sagittal axis, so that the long curved, bristled, and toothed setæ point forward. Abdomen and furca long.

Female.—Abdomen 3-jointed, slightly compressed laterally. The left arm of the furca is sharply compressed laterally at its base; otherwise the furca and abdomen are symmetrical. Genital segment enlarged, slightly rounded with a rounded prominence on each side of the genital opening. Anal segment with an acute strong dorsal spine. Each arm of the furca is fringed with soft bristles along the distal half of its inner edge, and has the full number of setæ. Five of these are plumose and unjointed, and one, the dorsal seta, projects upward from the plane of the others and is naked and jointed near the base. The third seta from the inside is longer than the majority and its projecting end bears stiff, long bristles which are more scattered than the others, and are attached at different angles. Feet of the fifth pair 2-jointed, alike (Fig. 15). First joint oblong with a plumose bristle on the outer edge near the end; terminal joint slightly narrower than the first, with four short, broad spines, one near the middle of the outer edge and three at the apex.

Male.— Gripping antenna powerful; distal section of two joints, middle section of six joints; of these, the second and fourth have a seta at the distal end, and the fifth and sixth and the first joint beyond the hinge have each a ridge which is finely toothed and ends in a spine. Abdomen of five joints (Fig. 12). The right side of the edge of the second joint is enlarged into a tubercle

which bears one or two minute spines. The anal segment is very short and has a dorsal spine similar to that of the female (Fig. 13). The right arm of the furca is slightly broader and longer than the left and bears upon its outer edge near the middle a tuft of from



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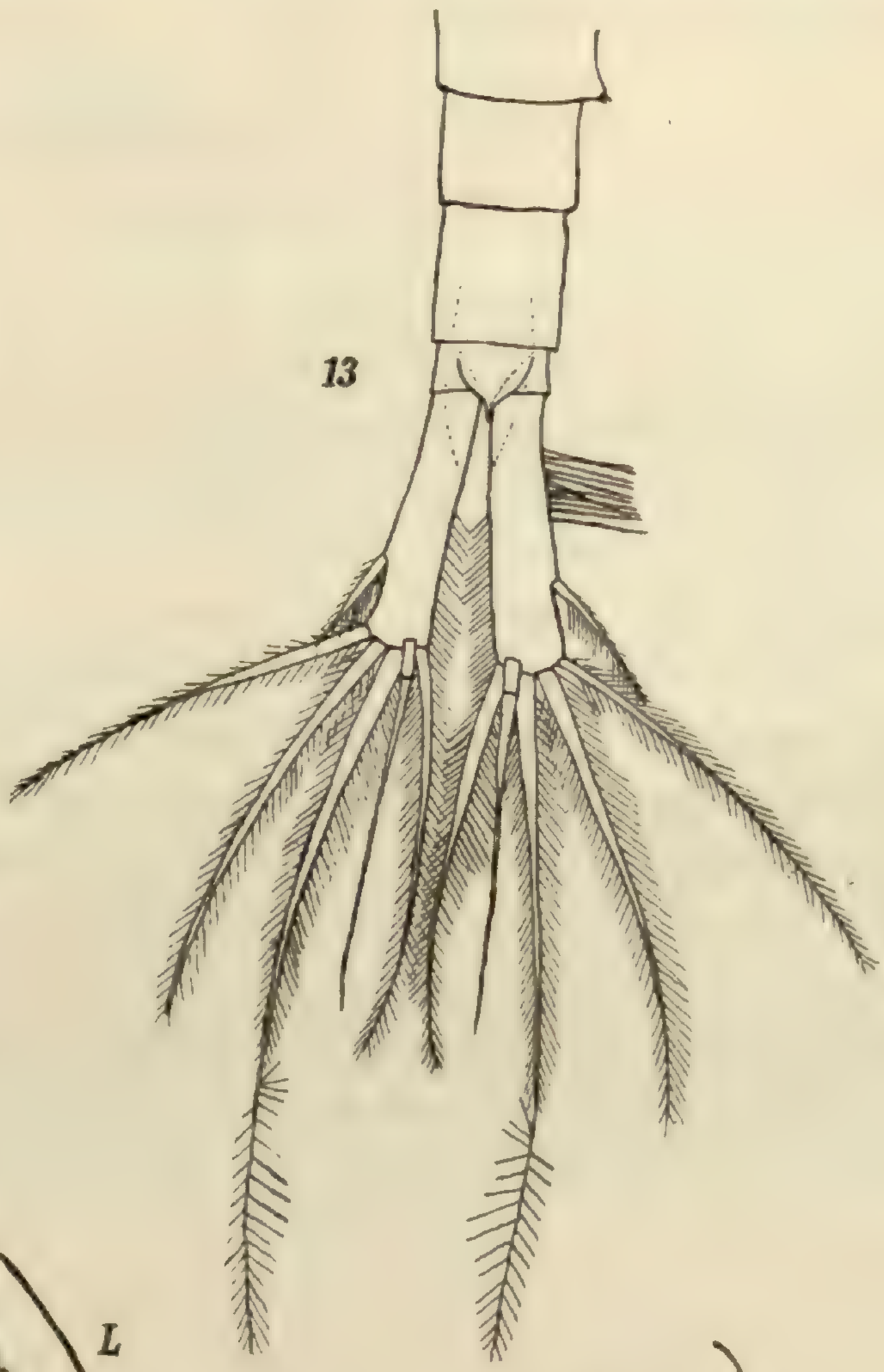

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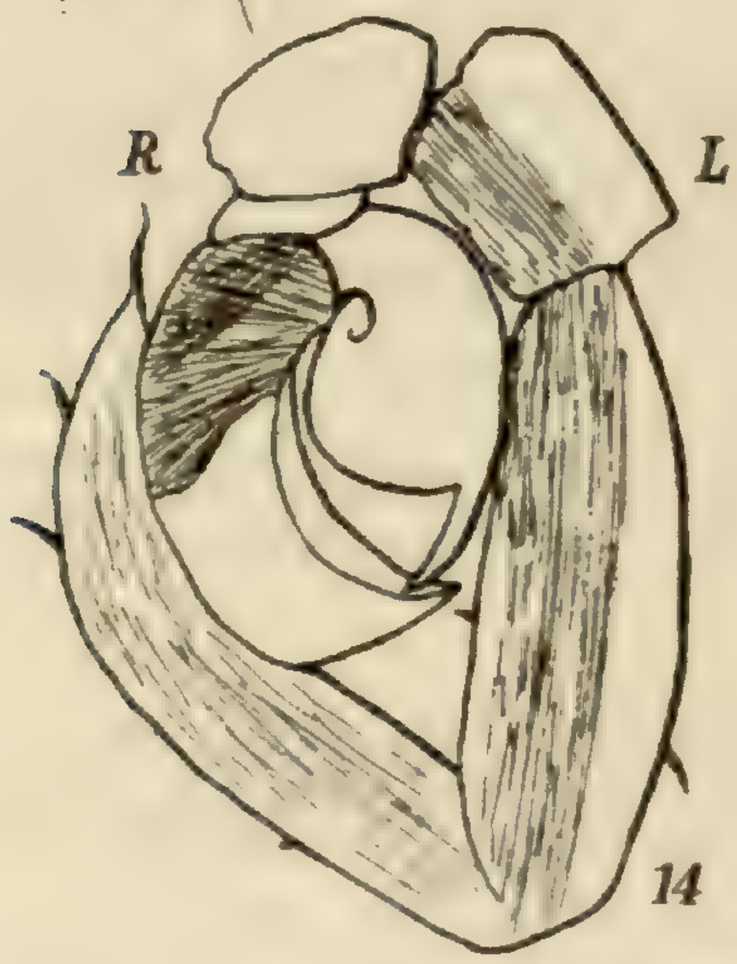

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Tortanus setacaudatus

Fig. 12.— Dorsal surface of male. x 75.
Fig. 13.— Dorsal surface of male abdomen. x 172.
Fig. 14.— Fifth feet of male, anterior surface. x 272.
Fig. 15.—Fifth feet of male, posterior surface. x 395.

12 to 20 stiff, slender bristles which form a conspicuous brush. The furcal setæ and the hairs on the inner edge of the furca are as in the female. Left fifth limb 3-jointed, more than twice the length of the right (Fig. 14). Basal joint nearly as broad as long; the second joint long, with one or more bristles on the inner and outer edges; distal joint arcuate, pointed, nearly as long as the other two, and with three recurved bristles on the outer and one on the inner edge. Right fifth limb is 3-jointed, the last two joints forming a heavy pincer; the second joint is spoon-shaped and receives a curved spine borne on the lower (anterior) side of the end of the swollen terminal joint.

Length of female 1.40 mm., of male 0.94 mm.

Abundant in Narragansett Bay and Charlestown Pond.

This is the second species of Tortanus to be described from the eastern coast of North America. *T. discaudatus* Thompson and Scott ('98) from the Gulf of St. Lawrence is very similar to this species. *T. bumpusii* Wheeler (:00) was found in Vineyard Sound and is apparently *T. discaudatus*.

Oithona plumifera Baird

1843. *Oithona plumifera* Baird.
1892. *Oithona plumifera* Giesbrecht.
1900. *Oithona plumifera* Wheeler.

Narragansett Bay, February.

Oithona similis Claus

1866. *Oithona similis* Claus.
1892. *Oithona similis* Giesbrecht.
1900. *Oithona similis* Wheeler.

Narragansett Bay at Wickford, June.

Longipedia coronata Claus

1863. *Longipedia coronata* Claus.
1880. *Longipedia coronata* Brady.
1898. *Longipedia coronata* Thompson and Scott.
1903. *Longipedia coronata* Sars.

Narragansett Bay and Charlestown Pond, summer. We have found no American record for this species.

Ectinosoma normani T. and A. Scott

1896. *Ectinosoma normani* T. and A. Scott.
1903. *Ectinosoma normani* Sars.

Charlestown Pond, summer. A species recorded from Norway, Scotland, and Ceylon.

Ectinosoma curticorne Boeck

1872. *Ectinosoma curticorne* Boeck.
1895. *Ectinosoma curticorne* Thompson.
1903. *Ectinosoma curticorne* Sars.

Charlestown Pond. One of the most common copepods in July and August. It has been previously reported from Norway, Scotland, and Spitzbergen.

Microsetella norvegica (Boeck)

1864. *Setella norvegica* Boeck.
1873. *Ectinosoma atlanticum* Brady and Robertson.
1890. *Ectinosoma atlanticum* Brady.
1892. *Microsetella atlantica* Giesbrecht.
1898. *Ectinosoma atlanticum* Thompson and Scott.
1903. *Microsetella norvegica* Sars.

Narragansett Bay, March. This species is cosmopolitan, with a wide distribution in the Atlantic Ocean and occurs in the Arctic, the Pacific, the Mediterranean, the Red Sea, and the Indian Ocean.

Tachidius littoralis Poppe

1881. *Tachidius littoralis* Poppe.
1895. *Tachidius littoralis* Thompson.

Narragansett Bay. Abundant in March and April.

Tachidius brevicornis (Müller)

1776. *Cyclops brevicornis* Müller.
1853. *Tachidius brevicornis* Lilljeborg.
1880. *Tachidius brevicornis* Brady.
1882. *Tachidius discipes* Giesbrecht.

Charlestown Pond, summer.

Parategastes sphæricus (Claus)

1863. *Amymone sphærica* Claus.
1866. *Amymone sphærica* Claus.
1880. *Amymone sphærica* Brady.
1903. *Tegastes sphæricus* Norman.
1904. *Parategastes sphæricus* Sars.

Charlestown Pond, abundant in July. The hand of the second maxilliped in these specimens is somewhat heavier than in the European species and resembles that of *Tegastes grandimanus*. Otherwise the agreement is complete.

Diosaccus tenuicornis (Claus)

1863. *Dactylopus tenuicornis* Claus.
1872. *Diosaccus tenuicornis* Boeck.
1873. *Nitokra tenuicornis* Brady and Robertson.
1880. *Diosaccus tenuicornis* Brady.

Charlestown Pond, July.

Dactylopusia vulgaris G. O. Sars.

1850. *Canthocamptus stromii* Baird.
1863. *Dactylopus cinctus* Claus.
1880. *Dactylopus stromii* Brady.
1903. *Dactylopusia vulgaris* Sars.

Charlestown Pond, July.

Thalestris serrulata Brady

1880. *Thalestris serrulata* Brady.
1895. *Thalestris serrulata* Thompson.
1898. *Thalestris serrulata* Thompson and Scott.

One female of this somewhat rare species was taken by scraping piles at high tide at Rocky Point in Narragansett Bay. Thompson and Scott have reported it from the American coast.

Harpacticus uniremis Kröyer

1845. *Harpacticus uniremis* Kröyer.
1903. *Harpacticus uniremis* Sars.

Narragansett Bay, abundant in February, March, and April; Charlestown Pond, July. Females in egg were found in both the summer and winter tows, though the largest number of specimens in copula were taken in March and April. The species was found in great abundance in shallow water and not, as Sars reports of the Norwegian specimens, confined to depths of from twenty to a hundred fathoms.

Harpacticus chelifer (Müller)

1776. *Cyclops chelifer* Müller.
1834. *Harpacticus chelifer* Milne-Edwards.
1880. *Harpacticus chelifer* Brady.
1903. *Harpacticus chelifer* Sars.

Charlestown Pond, July.

Idya furcata (Baird)

1837. *Cyclops furcatus* Baird.
1863. *Tisbe furcata* Claus.
1864. *Idya furcata* Boeck.
1880. *Idya furcata* Brady.
1903. *Idya furcata* Sars.

Narragansett Bay, spring. This is a very common Norwegian copepod and is "ubiquitous in the British seas" to quote Dr. Brady. It is also found in the Mediterranean, the Red Sea, and in New Zealand.

Argulus laticauda Smith

1874. *Argulus laticauda* Smith.
1903. *Argulus laticauda* Wilson.
1904. *Argulus laticauda* Wilson.

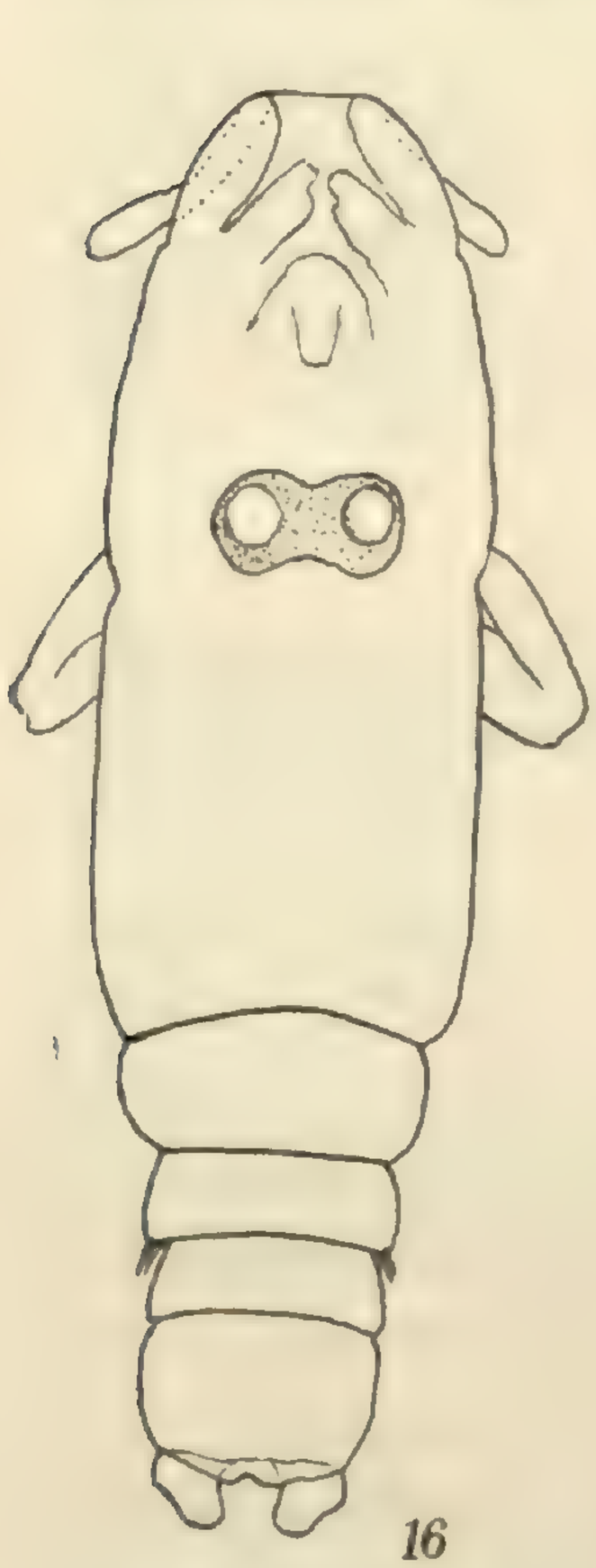
Charlestown Pond on tautog (*Tautoga onitis*).

Metanauplius of Caligus or Lepeophtheirus

Figs. 16–23

Two specimens of this metanauplius were taken near the surface, one on January 13 on the east side of the upper part of

Narragansett Bay (Crescent Park), the other a week later on the opposite side of the bay (Pawtuxet). They resemble in general the metanauplius raised from the eggs of *Caligus bonito* by C. B. Wil-



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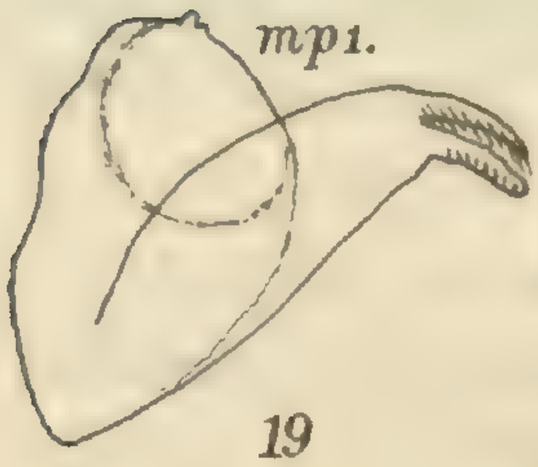

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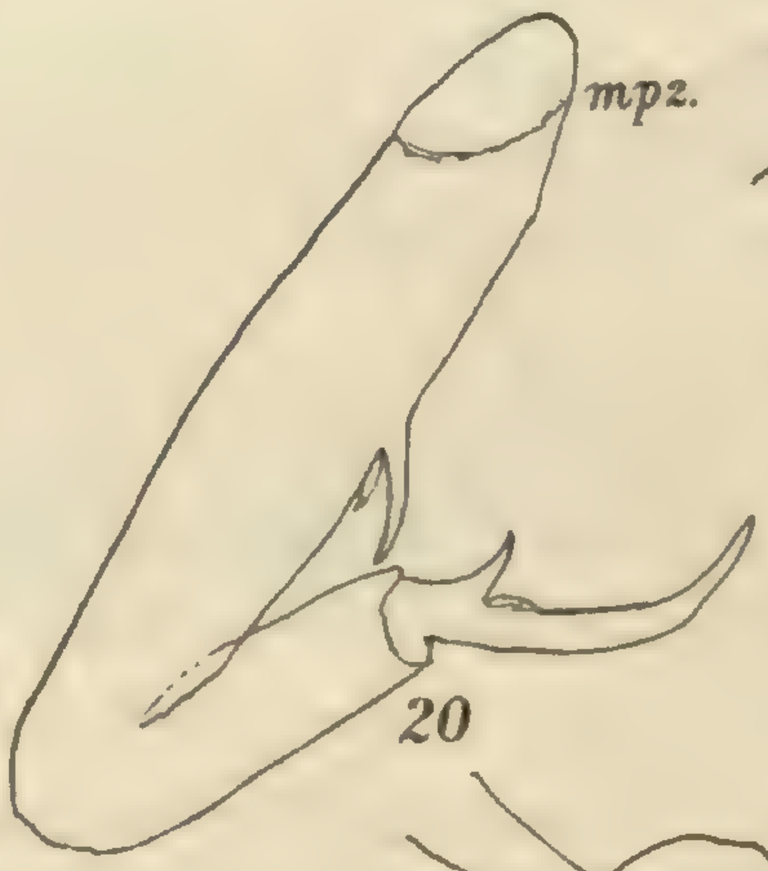

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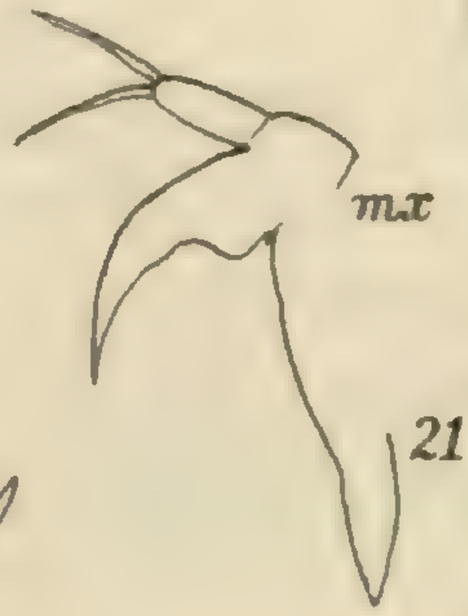

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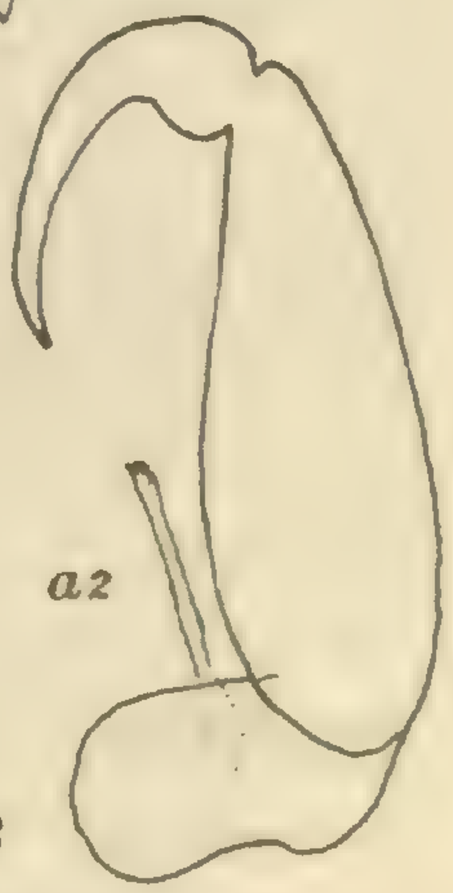

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Metanauplius of Caligus or Lepeophtheirus

FIG. 16.— Dorsal view. x 123.
FIG. 17.— Second foot, left. x 345.
FIG. 18.— Left arm of furca. x 345.
FIG. 19.— Right first maxilliped. x 345.
FIG. 20.— Right second maxilliped. x 345.
FIG. 21.— Right maxilla or mandible. x 345.
FIG. 22.— Left first antenna. x 345.
FIG. 23.— Left second antenna. x 345.

son (*Proc. U. S. Nat. Mus.*, vol. 28, figs. 40–45, 1905). Professor Wilson says of my specimens it is "the first instance on record where one has been obtained in its free habitat." The capture proves his inference that the metanauplius is free-swimming. However, even the genus cannot be positively identified since Professor Wilson's metanauplius is the only one as yet recognized. (The two specimens described by Brady ('99) from Otago, New Zealand, and named provisionally *Centromma thomsoni*, are very like my specimens and must belong to the Caligidæ rather than to the Corycæidæ.)

Length 0.63 mm.; breadth 0.157 mm.

The carapace is moderately slender and is marked near the middle by a slight notch on each side (Fig. 16). In front of these notches lie the eyes, the two pairs of antennæ, the protrusive toothed proboscis, the maxilla (?), and two maxillipeds. There seems to be a groove or depression in the dorsal surface of the carapace which runs backward from the front almost to the eyes. The ruby-red eyes are fused and lie just in front of the notches of the carapace. The first antenna (Fig. 22) arises some distance from the anterior end of the carapace and passes forward to its tip, then turns backward and downward towards its origin, and finally outward. The first portion seems to consist of two joints: a basal joint which is not clearly marked off from the carapace and which bears at its outer distal angle a strong spine, and a distal joint which is about twice the length of the first. The second portion is formed of two joints: a long one which bears two bristles and a short joint whose end is drawn out on the side next the carapace (outer side) into a long bristle. The distal portion of the antenna is a single joint which seems to be held almost at right angles to the sagittal axis of the metanauplius. Its end bears ten or twelve (or more) bristles, most of which are long and all non-plumose and flaccid. The second antenna (Fig. 23) is biramous. The basal joint is short and broad, and lies just inside that of the first antenna. The inner ramus is slender and relatively short, and ends in a tuft of four or more unjointed spines. The outer ramus is 2-jointed. The proximal joint is moderately swollen at the base but tapers distally. The distal joint is a hook swollen at the base.

On each side of the mouth there is the structure represented in Fig. 21 whose identity is not clear but which probably represents the maxilla. It is a ridge which bears in front a 2-jointed appendage and ends posteriorly in a strong spine. The basal joint of the appendage is drawn out posteriorly into a curved spine, swollen at base. It is possible that this represents the outer ramus and the basal portion of the appendage. The distal joint is oval, outwardly directed, and ends in two strong bristles. The first maxilliped (Fig. 19) is 2-jointed, heavy and short. The distal joint terminates in two claws, of which the outer is bristled and the inner finely toothed or bristled. The second maxilliped (Fig. 20) is 3-jointed. The basal joint bears near the middle of its inner surface a strong, backwardly directed spine. The second joint is about one half as long as the first. The distal joint is a sickle-shaped hook with a spine at base. The mouth is supplied with a protrusible proboscis which is a truncated cone armed at the apex with a circle of inwardly directed spines. This suggests that the metanauplius is ready to attach itself to a host.

At the posterior end, the carapace bears a pair of swimming legs. The first of the free thoracic segments bears a pair of legs and the second has on each side two spines. Two segments follow, the first without appendages, and the second, the anal segment, with the short furca. The two pairs of legs are very similar. Each has a single basal joint and two 1-jointed rami. There is a feathered bristle on the tip of the outer edge of each basal joint. The outer ramus of the first pair of swimming feet has four spines, one at the outer side and three at the end, and three long feathered bristles. The inner ramus has a smooth outer edge which bears an unjointed spine at the end. The inner edge has six (or seven) long feathered bristles. The second pair of legs (Fig. 17) is similar except that the outer ramus has three spines and four bristles and the inner ramus is broader than in the first pair. Each anal lamella (Fig. 18) (ramus of the furca) is short and irregular, and bears five bristles. The outer furcal seta is plumose on the outer side and the inner seta is plumose on both edges.

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BROWN UNIVERSITY

LICHENS OF MOUNT MONADNOCK, NEW HAMPSHIRE

REGINALD HEBER HOWE, JUNIOR

Mt. Monadnock (3166 feet), the typical representative of the monadnock type of worn-down mountain, is situated in the south-eastern corner of Cheshire County, N. H., in the townships of Jaffrey and Dublin. It rises from well watered, rolling meadow and woodland country of the Transition zone, and though surrounded by several prominent hills, Gap (1900 feet) for example, it stands well isolated. The lower slopes of the mountain are covered with upland pastures and woodlots, while between the altitudes of 2000 and 3000 feet of the Sub-Canadian zone, its sides are well wooded with both coniferous and deciduous growths. Above 3000 feet the fauna and flora of its weathered, rounded, and rocky summit of resistant ledges are characteristic of the Canadian zone.

The lichens here listed were collected on April 5, 1906, about the base of the mountain on the Troy side, and on Bigelow Hill (1702 feet), and again on April 6, 1906, during one ascent to the summit of Monadnock itself.

Examples of all specimens listed are in my herbarium. For the verification of determinations of the genus Cladonia, and of several other specimens I am indebted to the kindness of Professor Bruce Fink of Grinnell, Iowa. To Mr. Rollin M. Gallagher I am also indebted for assistance in collecting.

1. **Ramalina calicaris fraxinea** Fr.—One specimen collected on a cherry tree, Bigelow Hill. Fertile.

2. **Ramalina calicaris fastigiata** Fr.—Common in the Transition zone. Found on cherry, elm, and on Bigelow Hill on a rock. Fertile.

3. **Ramalina calicaris canaliculata** Fr.—One specimen collected on an elm, Bigelow Hill. Fertile.

4. **Ramalina calicaris farinacea** Schaer.—One old wall had several patches on individual rocks. Transition zone. Sterile.

5. **Cetraria islandica** (L.) Ach.—Common in a reduced state on the ledges near the summit. Sterile.

6. **Cetraria ciliaris** (Ach.).—Not uncommon on pines near the base. Fertile.

7. **Cetraria lacunosa** Ach.—Common on pines on Bigelow Hill and about the base of the mountain; rare in the Sub-Canadian zone. Fertile.

8. **Cetraria oakesiana** Tuck.—Common in the Sub-Canadian zone on dead wood, yellow birch, oaks, and in one instance on rock. Sterile.

9. **Cetraria juniperina pinastri** Ach.—A few examples on a fallen spruce at timber line. Sterile.

10. **Evernia prunastri** (L.) Ach.—Common in the Transition zone, rare in the Sub-Canadian. Found growing on old roofs, stone wall, on *Parmelia perlata* on rock, and on deciduous trees. Sterile.

11. **Usnea barbata florida** Fr.—Uncommon on oaks on Bigelow Hill. Sterile.

12. **Usnea barbata florida rubiginia** Michx.—Bigelow Hill. Uncommon on oaks. A small but fairly typical specimen was collected on a rock, which proves that the coloring is not due to tannin or some other vegetable coloring matter in the bark of trees as has been suggested. Sterile.

13. **Usnea barbata ceratina** Schaer.—One untypical specimen collected on an oak on Bigelow Hill. Sterile.

14. **Alectoria jubata chalybeiformis** Ach.—A single specimen was collected on Bigelow Hill on the ground, growing with Cladonias.

15. **Theloschistes concolor effuse** Tuck.—Two small specimens on oak on Bigelow Hill.

16. **Parmelia perlata** (L.) Ach.—Common on rocks throughout the Transition and Sub-Canadian zone. Fertile in two instances.

17. **Parmelia cetrata** Ach.—Two examples on oak on Bigelow Hill.

18. **Parmelia crinita** Ach.—One example growing on moss on apple tree. Bigelow Hill. Sterile.

19. **Parmelia tiliacea** (Hoffm.) Floerk.— Common throughout Transition and Sub-Canadian zones. Collected on apple and yellow birch. Fertile.

20. **Parmelia borreri rudecta** Tuck.— Common in Transition and Sub-Canadian zones. Collected on yellow birch. Sterile.

21. **Parmelia saxatalis** (L.) Fr.— Not uncommon on rock. Transition zone. Fertile.

22. **Parmelia saxatalis sulcata** Nyl.— Common in both Transition and Sub-Canadian zones, growing on trees and rock. Sterile.

23. **Parmelia physodes** (L.) Ach.— Common throughout both Transition and Sub-Canadian zones, but more common in the latter. One example fertile. Collected on trees, and rarely on rocks.

24. **Parmelia olivacea** (L.) Ach.— Common in Sub-Canadian zone on yellow birch and oak. Fertile.

25. ? **Parmelia olivacea sorediata** (Ach.) Nyl.— One specimen collected on a white pine at the base of the mountain seems referable to this form.

26. **Parmelia caperata** (L.) Ach.— Common in Transition zone, more rarely met with in the Sub-Canadian. Collected both on rocks and on trees. Sterile. When found growing vertically on rocks this species has a deceptive shredded appearance.

27. **Parmelia conspersa** (Ehrh.) Ach.—Common throughout the two lower zones growing on rocks, replaced by the following species above timber line. Fertile.

28. **Parmelia centrifuga** (L.) Ach.— Not uncommon above timber line, confined mainly to the highest ledges. One example fertile.

29. **Physcia pulverulenta leucoleiptes** Tuck.— Common in the Transition zone on apple trees. Sterile.

30. **Physcia stellaris** (L.).— Common both on rocks and trees. Fertile.

31. **Physcia stellaris aipolia** Nyl.— One example collected on a rock. Bigelow Hill. Sterile.

32. **Physcia tribacea** (Ach.) Tuck.— One example collected on rock on Bigelow Hill. Fertile.

33. **Physcia obscura endochrysea** Nyl.— Common on yellow birch in the Sub-Canadian zone. Sterile.

34. **Pyxine sorediata** Fr.—Not uncommon on beech in Sub-Canadian zone. Sterile.

35. **Umbilicaria hyperborea** Hoffm.—Found both on the top of Bigelow Hill on boulders, and on the summit ledges of Monadnock.

36. **Umbilicaria muhlenbergii** (Ach.) Tuck.—Growing on pasture rock at the base of the mountain. Fertile.

37. **Umbilicaria dillenii** Tuck.—Common on ledges in the Sub-Canadian zone.

38. **Umbilicaria pennsylvanica** Hoffm.—Several specimens were collected on ledges at about 2500 feet elevation. Fertile.

39. **Umbilicaria pustulata papulosa** Tuck.—Common on pasture rocks and on the mountain ledges nearly to the summit. Fertile.

40. **Sticta amplissima** (Scop.) Mass.—Common on yellow birch on the mountain and also on rocks on Bigelow Hill. Fertile.

41. **Sticta pulmonaria** (L.) Ach.—Common in both Transition and Sub-Canadian zones on oaks and yellow birch, and in a few instances on rocks. Sterile.

42. **Nephroma tomentosum** (Hoffm.) Koerb.—One example on rock in Sub-Canadian zone. Fertile.

43. **Nephroma lævigatum** Ach.—One example on rock, Sub-Canadian zone. Fertile.

44. (?) **Peltigera canina** (L.) Hoffm.—On ground over ledges, not uncommon. Bigelow Hill. Sterile.

45. **Pannaria lanuginosa** (Ach.) Koerb.—Common on rocks in the two lower zones. Sterile.

46. **Ephebe solida** Born.—One example on rock, Bigelow Hill. Determined through the kindness of Dr. Herbert M. Richards of Barnard College, N. Y.

47. **Leptogium tremelloides** (L. fil.) Fr.—One example on rock, Sub-Canadian zone. Sterile.

48. **Placodium vitellinum** (Ehrh.) Noeg. & Hepp.—One example on old barn, Transition zone. Fertile.

49. **Lecanora rubina** (Vill.) Ach.—Common on rock on Bigelow Hill. Fertile.

50. **Lecanora subfusca** (L.) Ach.—One example on yellow birch. Fertile.

51. **Lecanora pallescens** (L.) Schaer.—One example on yellow birch in Sub-Canadian zone. Fertile.

52. **Pertusaria velata** (Turn.) Nyl.—One example on oak. Bigelow Hill. Fertile.

53. **Stereocaulon paschale** (L.) Fr.—Common on rocks in Sub-Canadian zone. Fertile.

54. **Stereocaulon tomentosum** (Fr.) Th. Fr.—One example on rock in Sub-Canadian zone. Fertile.

55. (?) **Cladonia cariosa** (Ach.) Spreng.—One example on ground, Sub-Canadian zone. "An unusual form to be studied further."—Fink.

56. **Cladonia pyxidata** (L.) Fr.—Common, Sub-Canadian zone.

57. **Cladonia fimbriata nemoxyne** (Ach.) Coem.—Two examples, mossy ground and old stump, Sub-Canadian zone.

58. **Cladonia fimbriata coniocræa** (Floerk) Wain.—One example on ground, Sub-Canadian zone.

59. **Cladonia squamosa** Hoffm.—One example on ground, Sub-Canadian zone.

60. **Cladonia furcata** (Huds.) Fr.—Common on ground, Sub-Canadian zone.

61. **Cladonia furcata** (**racemosa** Fl. or **pinnata** (Fl.) Wain.?)—One example on ground, Sub-Canadian zone.

62. **Cladonia rangiferina** (L.) Hoffm.—Abundant on ground in all three zones.

63. **Cladonia rangiferina sylvatica** L.—Common on ground, particularly in the two lower zones.

64. **Cladonia amaurocræa** (Fl.) Schaer. (**furcata**?).—Common on ground between ledges in Canadian zone.

65. **Cladonia uncialis** (L.) Fr.—One example on ground, Canadian zone.

66. **Cladonia boryi** Tuck.—Common on ground in a reduced condition in Canadian zone.

67. **Cladonia** (**Cornucopoides**) **coccifera** (L.) Willd.—Common on ground in Sub-Canadian zone.

68. **Cladonia coccifera pleurota** (Fl.) Schaer.—One example on ground, Sub-Canadian zone.

69. **Cladonia bacillaris** Nyl.—One example on fallen stump on ground, Sub-Canadian zone.

70. **Cladonia cristatella** Tuck.—Common in two lower zones.

71. **Graphis scripta** Ach.—One example on beech, Sub-Canadian zone.

NOTES AND LITERATURE

BOTANY

Notes.— A monograph of Primulaceæ, by Pax and Knuth, forms Heft 22 of Engler's *Das Pflanzenreich.*

An account of a large white elm, with figures, is given by Williams in *Forest Leaves* for February.

A case of trunk-grafting of the elm is illustrated in *Sports Afield* for February.

An interesting series of Rumex illustrations, including hybrids, is being published in vol. 24 of Reichenbach's *Icones Floræ Germanicæ et Helveticæ.*

The Camus monograph of the willows of Europe has recently been completed by the issuance of a second part, with atlas, from the Lechevalier House, of Paris.

Engler revises the pothoid Araceæ in Heft 21 of *Das Pflanzenreich.*

The rediscovery of *Cypripedium fairieanum* is sketched by Barron in *The Garden Magazine* for March.

A domestically interesting Aloe, from Angola, is described by Berger in the *Journal of Botany* for February.

Foliage anatomy and its classificatory value in Festucaceæ are considered by Luerssen in Heft 63 of *Bibliotheca Botanica.*

A series of photographic illustrations of agriculturally interesting grass glumes is given by Neubauer in *Landwirtschaftliche Jahrbücher* for December 18.

Sorghum halepense, like *S. vulgare*, is said to yield hydrocyanic acid sometimes under the influence of enzymes, by Crawford, in *Bulletin no. 90, part 4*, of the Bureau of Plant Industry, U. S. Department of Agriculture.

A popular note on evergreens, with some Conifer illustrations, is published by Maynard in *Suburban Life* for February.

A reprint of the Lloyd edition of "Travels in the Interior of North America," by Maximilian, Prince of Wied (London, 1843) is being issued as volumes 22 to 24 of Thwaites' *Early Western Travels: 1748–1846* — with atlas.

An account of the forest belts of western Kansas and Nebraska, by Kellogg, forms *Bulletin no. 66*, Forest Service, of the U. S. Department of Agriculture.

An account of the wild and cultivated Amaryllidaceæ of Argentina is given by Holmberg in vol. 5 of the current series of *Anales del Museo Nacional de Buenos Aires.*

An interesting account of the macroplankton, or free-floating archegoniates and spermatophytes of the pools of Paraguay is given by Chodat in the *Bulletin de l'Herbier Boissier* of January 31.

An Enumeration of the Vascular Plants known from Surinam, Together with their Distribution and Synonymy, by Pulle, has been issued from the Brill press of Leiden.

A dichotomous key to French plants has been published by Léveillé (Paris, Chas. Amat, 1906), in convenient pocket form.

A monograph of the Aconites of India, by Stapf, forms vol. 10, part 2, of the *Annals of the Royal Botanic Garden, Calcutta.*

The utilization of seaweeds of the United States is considered by Smith in vol. 24 of the *Bulletin of the Bureau of Fisheries.*

Mushrooms and their cultivation form the subject of a well illustrated article by McAdam in *Country Life in America* for February.

A paper on the Russulas of Madison and vicinity, by Denniston, has been separately printed from vol. 15 of the *Transactions of the Wisconsin Academy.*

A note on the poisoning of cattle in Manitoba by *Amanita muscaria* and a species of Boletus is published by Criddle in *The Ottawa Naturalist* for February.

A brief account of the mechanism by which Salix, Cladrastis, Tilia, and other woody genera discard their terminal buds in a characteristic manner, is given by Tison in *Comptes Rendus . . . . de l'Académie des Sciences* of Paris for January 22.

Weevil-resisting characters in cotton, some of them connected with the "kelep" ant, form the subject of *Bulletin no. 88* of the Bureau of Plant Industry, U. S. Department of Agriculture, by Cook.

An account of some phases of the ecology of plants of the extreme north has recently been issued by Haglund, of Upsala.

A list of wild medicinal plants of the United States, by Alice Henkel, forms *Bulletin no. 89* of the Bureau of Plant Industry, U. S. Department of Agriculture.

The botanical treatment in the new *National Standard Dispensatory* (Lea Brothers & Co., 1905) is by Rusby.

An economic account of *Mentha piperita* and its varieties is given by Alice Henkel in *Bulletin no. 90, part 3*, of the Bureau of Plant Industry, U. S. Department of Agriculture.

An account of the Japanese lac derived from Rhus is given by Stevens in *The American Journal of Pharmacy* for February.

Mayer, in *Landwirtschaftliche Jahrbücher* of December 18, gives a translation of an article by Giltay on the method of teaching botany in the agricultural academy at Wageningen.

A biographic sketch of Errera, by Massart, with an excellent portrait and a list of his publications, has been issued from the Hayez press of Brussels.

An illustrated account of the Desert Botanical Laboratory at Tucson is contributed by Cannon to *Out West* for January.

The third annual issue of part M, Botany, of the *International Catalogue of Scientific Literature* was issued in September by the Royal Society of London,— the manuscript having been completed in February last. It forms an octavo volume of 909 pages.

A photographically illustrated article on soil formation, by Fletcher, is published in *Country Life in America* for January.

Pammel has distributed an interesting paper comparing certain swamp, clay, and sandstone floras,— separately printed from vol. 10 of the *Proceedings of the Davenport Academy of Sciences.*

The flora of one of the "Chouteau buttes" of Missouri is analyzed by Standley in vol. 1, part 2, of the *Bulletin of the Bradley Geological Field Station* of Drury College.

A list of additions and corrections to Fleet's list of Mt. Rainier plants is published by Piper in *Mazama* of December last.

An illustrated account of the vegetation of the Bahamas, with a list of the species so far known as occurring on them, is separately

issued by the author, Professor Coker, from Shattuck's *The Bahama Islands*, published by the Geographical Society of Baltimore.

The concluding parts of Macloske's "Flora Patagonica," forming part 5 of volume 8 of the *Reports of the Princeton University Expeditions to Patagonia, 1896–1899*, have recently been issued.

A paper on the alpine flora of northern Argentina, by R. E. Fries, is published as the opening number of series 4, vol. 1, of the *Nova Acta R. Societatis Scientiarum Upsaliensis*.

The third of Merrill's papers on "New or Noteworthy Philippine Plants," and a paper on the source of Manila "elemi," form no. 29 of the publications of the *Bureau of Government Laboratories*, of Manila.

The *Flora of Tropical Africa*, under the editorship of Sir William T. Thiselton-Dyer, reaches into Convolvulaceæ in the recently issued vol. 4, sect. 2, part 1.

An account of the botany of northwestern New South Wales is given by Turner in vol. 30 of the *Proceedings of the Linnean Society* of that country.

A colored plate of *Sarracenia flava* accompanies an article on the genus in *Flora and Sylva* for November.

An illustrated account of garden Sarracenias, by Vollbracht, is published in the *Wiener Illustrierte Garten-Zeitung* for December.

An illustrated monograph of the Uromyces forms of Bauhinia is published by Westergren in no. 4 of the *Arkiv för Botanik* of 1905.

Data on the bud-rot of Cocos are given in vol. 6, no. 3, of the *West Indian Bulletin*.

Vol. 22, part 2 (the second fascicle issued), of the *North American Flora* under the editorship of Professors Underwood and Britton, includes Saxifragaceæ (Small), Hydrangeaceæ (Rydberg), Cunoniaceæ, Iteaceæ, Hamamelidaceæ (Britton), Pterostemonaceæ (Small), Altingiaceæ (Wilson), and Phyllonomaceæ (Rusty). It bears date December 18.

A geographic-systematic account of North American Saxifraginæ is published by Rosendahl as a supplement to vol. 37, part 2, of Engler's *Botanische Jahrbücher*, issued in December.

A new northern Antennaria is described by Greene in *The Ottawa Naturalist* of January.

Habit and bark photograms of *Quercus rubra* are published in *Forest Leaves* for December.

The *Journal of Botany* for January contains a revision of Ceratostigma by the new Director of the Kew Gardens, Col. Prain.

The geographic distribution of Ulmaceæ is being analyzed by Bernard in current numbers of the *Bulletin de l'Herbier Boissier*.

An analysis of the subgenera of Ribes, with a detailed account of the first of these, Parilla, is separately issued by Janczewski from the *Bulletin International de l'Académie des Sciences de Cracovie*.

Dahlstedt gives an illustrated account of the Scandinavian forms of Taraxacum in *Botaniska Notisser* for 1905.

Floral teratology in two species of Salix is discussed by Mott in vol. 2, no. 7, of the *University of California Publications, Botany*.

A monograph of the willows of Ohio, by Griggs, forms vol. 4, part 6, of the *Proceedings of the Ohio State Academy of Science*.

Two new aloes are described and figured by Schönland in the *Gardeners' Chronicle* of December 2.

Kinetostigma is the name proposed by Dammer, in no. 36 of the *Notizblatt des k. botanischen Gartens und Museums zu Berlin*, for a Chamædorea-like Guatemalan palm genus.

A. Usteri re-analyzes the morphology of the Coniferous ament in the light of some new Cunninghamia material, in the *Revista da Sociedade Scientifica de São Paulo* of September last.

Christensenia is proposed by Maxon, to replace the generic name Kaulfussia in Marattiaceæ, in the *Proceedings of the Biological Society of Washington* of December 9, in which he also describes a new Lycopodium from Guatemala.

The Fern Allies of North America North of Mexico is the title of a new book by Clute recently issued from the Stokes Press of New York. It is illustrated very fully and well.

Setchell gives an account of the parasitic Florideæ of California, in *Nuova Notarisia* for April.

A neat little pamphlet on "Lichenology for Beginners" has been separately printed from *The Bryologist* by F. L. Sargent, and is offered by the Harvard Coöperative Society of Cambridge.

The fungi of the Belgian Antarctic Expedition are described by Madame Bommer and Madame Rousseau in a separate recently issued from the Buschmann Press of Antwerp.

A paper on pathogenic species of Aspergillus is published by Constantin and Lucet in series 9, vol. 2, no. 1–3, of the *Annales des Sciences Naturelles, Botanique.*

A paper on the Pyrenomyceteæ of Orleans Co., N. Y., by Fairman, constitutes a brochure of vol. 4 of the *Proceedings of the Rochester Academy of Science,* recently issued.

An illustrated paper by House on the fungi and bacteria of plant diseases forms *Circular no. 18* of the Estacion Central Agronomica of Cuba.

An Alternaria rot of apples is described by Longyear in *Bulletin 105* of the Agricultural Experiment Station of Colorado.

A monograph of the apples of New York, by Beach, Booth, and Taylor, constituting part 2 of the *Report of the New York Agricultural Experiment Station for 1903,* recently issued, forms two octavo volumes, illustrated by numerous plain and colored plates.

Alcocer has begun the publication of a paper on the fruits of Mexico in current issues of the *Anales del Museo Nacional de Mexico.*

An illustrated popular account of the tobacco industry of the United States is given by Willey in *The American Inventor* for December.

Montgomery argues, in *The Popular Science Monthly* for January, that Zea and Euchlæna may have had a common origin, the central spike of a tassel-like structure developing into the ear in the former, and its lateral branches giving rise to the clustered pistillate spikes of teosinte.

Results of corn selection are given by Lyon in *Bulletin no. 91* of the Agricultural Experiment Station of Nebraska.

An account of raffia and its preparation, by Deslandes, has recently appeared from the press of Challamel of Paris.

A lecture on heredity and the origin of species, by MacDougal, is separately distributed from *The Monist* for January.

Notes on the Life History of British Flowering Plants is the title of a volume by Lord Avebury, recently issued from the Macmillan Press.

Harris's conclusions on the influence of Apidæ on the geographical distribution of certain floral types are restated in *The Canadian Entomologist*, October to December.

Foliage phenology in Ceylon is discussed by Wright in vol. 2, part 3, of *Annals of the Royal Botanic Gardens, Peradeniya.*

A portrait of the retiring Director of Kew Gardens, Sir W. T. Thiselton-Dyer, is published in the *Gardeners' Chronicle* of December 9.

A short biographic sketch of Tschirch, with portrait, is published in the *American Journal of Pharmacy* for January.

The October number of the *Nuovo Giornale Botanico Italiano* is dedicated to the memory of Delpino, whose portrait forms its frontispiece.

A catalogue of plants cultivated in the Vilmorin Gardens forms an appendix to the 1904 volume of the *Bulletin de la Société Botanique de France*,— recently issued.

The Journals.— *Botanical Gazette*, December:— Atkinson, "Life History of *Hypocrea alutacea*"; Transeau, "The Bogs and Bog Flora of the Huron River Valley"; Bergen, "Tolerance of Drought by Neapolitan Cliff Flora"; Lyon, "A New Genus of Ophioglossaceæ [Sceptridium]."

Botanical Gazette, January:— Chrysler, "The Nodes of Grasses"; Transeau, "The Bogs and Bog Flora of the Huron River Valley"; Merriman, "Nuclear Division in Zygnema"; Breazeale, "Effect of Certain Solids upon the Growth of Seedlings in Water Cultures"; Hitchcock, "Notes on North American Grasses — V"; Farmer, "Sporogenesis in Pallavicinia"; Moore, "Reply [to the foregoing]."

Bulletin of the Torrey Botanical Club, November: — Howe, "Phycological Studies — II"; Underwood, "The Genus Alcicornium of Gaudichaud"; Rydberg, "Studies on the Rocky Mountain Flora — XV"; Osterhout, "New Plants from Colorado"; Hastings, "Observations on the Flora of Central Chile."

Bulletin of the Torrey Botanical Club, December: — Murrill, "The Polyporaceæ of North America — XIII"; Rydberg, "Astragalus and its Segregates as Represented in Colorado."

Bulletin of the Torrey Botanical Club, January: — Evans, "Hepaticæ of Puerto Rico — VI"; Arthur, "New Species of Uredineæ — IV"; Underwood, "The Genus Stenochlæna"; Small, "Studies in North American Polygonaceæ — II."

The Bryologist, January: — Fink, "Edward Tuckerman — A Brief Summary of his Work" (with portrait); Merrill, "Lichen Notes No. 2"; Haynes, "*Cephalozia francisci*."

The Fern Bulletin, October: — Nichols, "*Schizæa pusilla* in Cape Breton"; Woolson, "A Precocious Cystopteris"; Gilbert, "Observations on North American Pteridophytes — II"; Klugh, "*Scolopendrium vulgare* in Ontario"; Davenport, "Reversions and their Fluctuations"; Gilbert, "Mrs. Taylor's Georgia Ferns"; Clute, "A Check List of the North American Fernworts."

The Iowa Naturalist, October: — Cratty, "The Juncaceæ of Iowa"; Fitzpatrick, "The Melanthaceæ of Iowa."

Journal of Mycology, September: — Morgan, "North American Species of Marasmius"; Beardslee, "The Amanitas of Sweden"; Kellerman, "Index to North American Mycology."

Journal of Mycology, November: — Morgan, "North American Species of Marasmius" (*continued*); Atkinson, "The Genera Balansia and Dothichloë in the United States, with a Consideration of their Economic Importance"; Sumstine, "Another Fly Agaric"; Holway, "Notes on Uredineæ — IV"; Sturgis, "Remarkable Occurrence of *Morchella esculenta*"; Kellerman, "Notes from Mycological Literature — XVII."

Journal of the New York Botanical Garden, November: — Nash, "Further Explorations in the Republic of Haiti."

Journal of the New York Botanical Garden, December: — Murrill, "Collecting Fungi in Maine."

Journal of the New York Botanical Garden, January: — Berry, "Fossil Plants along the Chesapeake and Delaware Canal"; Nash, "The *Coco de Mer*, or Double Cocoanut"; Hollick, "Origin of the Amber found on Staten Island."

The Ohio Naturalist, December: — Gleason, "Notes from the Ohio State Herbarium — V"; Schaffner, J. H., "Key to the Ohio Dogwoods in the Winter Condition"; Schaffner, Mabel, "Free-Floating Plants of Ohio."

The Ohio Naturalist, January: — Tillman, "The Embryo-sac and Embryo of *Cucumis sativus*"; Kellerman, York, and Gleason, "Annual Report on the State Herbarium for the Years 1903, '04 and '05"; Sterki, "Some Notes on Martynia"; Hillig, "A New Case of Mutation [*Commelina nudiflora*]"; Schaffner, "Additional Observations on Self-pruning."

The Ottawa Naturalist, December: — Greene, "On so-called *Silene menziesii*"; Fernald, "An Alpine Variety of *Cnicus muticus*"; Fernald, "A New Goldenrod from the Gaspé Peninsula"; Macoun, "Two Rare Fungi [*Cyclomyces greeni* and *Pleurotus subareolatus*]."

The Plant World, October: — Leavitt, "The Defences of the Cock-spur Thorn"; Atkinson, "Outlines for the Observation of Some of the More Common Fungi" (*conclusion*); Gray, "Variations in Trillium."

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The following botanical papers, or abstracts of them, are contained in the *Report of the Eighth Geographic Congress* (Washington, Govt. Printing Office, 1905):—Cowles, "A Remarkable Colony of Northern Plants along the Apalachicola River, Florida. and its Significance"; Cowles, "The Importance of the Physiographic Standpoint in Plant Geography"; Harshberger, "Methods of determining the Age of the Different Floristic Elements of Eastern North America"; Drude, "Die Methode der pflanzen-geographischen Kartographie, erläutert an der Flora von Sachsen"; Anderson, "The Flora of Connaught as Evidence of the Former Connection with an Atlantic Continent"; White, "The American Range of the Cycadofilices."

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CONTENTS

		Page
I.	Naididæ of Cedar Point, Ohio . . . . PROFESSOR L. B. WALTON	683
II.	Mechanism of the Odontophoral Apparatus in *Sycotypus canaliculatus* J. C. HERRICK	707
III.	Notes and Literature: *Biology,* Loeb's Dynamics of Living Matter; *Zoölogy, Capture of the Salamander, Autodax lugubris, at Los Angeles, Cal.* (L. H. Miller), *Pimephales notatus in the Lower Susquehanna,* (H. W. Fowler), Notes; *Botany,* Notes, The Journals	789

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NAIDIDÆ OF CEDAR POINT, OHIO

L. B. WALTON

THE microscopic annelids constituting the family Naididæ of the subclass Oligochæta are a group which has received little attention in America. Michaelsen (:00) in his monograph of the Oligochæta recognized 42 species from various parts of the world and of that number only 6 were noted as occurring in our territory although observations made by Smith (:00) and noted in the appendix ("Zusätze und Berichtigungen") increased the number to 12. While this, taken in connection with the fact that the observations have been confined almost entirely to two localities, the one in Pennsylvania the other in Illinois, furnishes sufficient justification for a review of the Naididæ occurring at Cedar Point, Ohio, some contemplated studies of a statistical nature rendered a preliminary survey of several groups of fresh-water organisms desirable for the purpose of ascertaining which could be used most advantageously in the problems under consideration. Consequently the present paper is purely from a systematic standpoint, and although a considerable number of specimens have been fixed, stained, and mounted, and a few imbedded and sectioned, no attention beyond that necessary to differentiate the species has been given to anatomical or histological structure.

In addition to the interest attached to the study of these organisms upon the side of pure science, as outlined above, the fact that they play a *rôle* of decided economic importance must not be overlooked. The relation of the microscopic organisms or "plankton," accepting the definition in its broadest sense, to the

distribution of food fishes is a subject which has received increasing attention during the past twenty years. Inasmuch as the food of fishes is made up chiefly of small Crustacea, insect larvæ, minnows, etc., the existence of these being in turn dependent on microscopic forms, among which the Naids occupy an important position, it is evident that the distribution of such microscopic organisms controls to a large extent the fish supply in any given locality.

The somewhat unique location of Cedar Point with the open lake on the north and a portion of Sandusky Bay extremely rich in aquatic vegetation on the south, renders the Lake Laboratory situated there a station particularly well adapted to the study of the animal and plant life occurring in fresh water and to the investigation of the various problems of biological importance connected therewith.

The present study was carried on at the laboratory during a period of six weeks in July and August, 1905, the greater portion of the time, however, being occupied with other work. Consequently the record of species is undoubtedly far from complete, although 10 species, 7 of them new to science, are noted. The large proportion of new forms indicates the present condition in regard to the systematic study of the Naids in the United States, and while the writer has no wish to be classed as a "species maker," nevertheless it is important to lay the foundations for future biological studies by first considering those groups containing individuals resembling each other sufficiently well to be called "species."

The principal papers dealing with American Naids outside of the excellent monographs of Michaelsen (:00) and Beddard ('95), are those of Leidy ('50a, '50b, '52a, '52b, '80), Minor ('63), Reighard ('85), Cragin ('87), and Smith ('96 and :00). In addition to these, papers indispensable to the student of the group have been published by Beddard, Benham, Bourne, Bousfield, Bretschner, Michaelsen, Tauber, and Vejdovsky, that of the last author being classical in its morphological treatment of the forms. The majority of these papers are either in the library of the writer, or in the library of the department of biology of Kenyon College. Mention should here be made of the courtesies extended by the American Museum of Natural History, New York, the library

of Cornell University, and the Museum of Comparative Zoölogy of Harvard University, in the loan of literature otherwise inaccessible. I am furthermore greatly indebted to Samuel Henshaw of the Museum of Comparative Zoölogy for noting certain references.

The studies of the various species were made primarily from living specimens, all figures having been drawn with the aid of the camera lucida at the magnification noted in each instance. The most satisfactory method was that of transferring the Naid from the culture by means of a pipette to a watch-glass and subsequently to a drop of water on a slide, then placing over the drop a cover-glass the margin of which was supported by an extremely thin wooden wedge. After a time the specimens, without undue compression, would become quiet and outline drawings could be made with the camera. Specimens to be mounted were fixed with hot sublimate-alcohol (sublimate 10 g., absolute alcohol 100 cc., distilled water 100 cc., acetic acid 2 cc.), stained in borax-carmine, and eventually transferred to balsam, while those sectioned were stained in hæmatin IA (Apathy) or in iron-hæmatoxylin (Heidenhain) after fixation in cold sublimate-alcohol. The index of refraction of balsam approaches so closely the refraction of the transparent setæ that in order to study them most advantageously it was found advisable to kill the specimens by compressing them under the cover-glass and then at once to make camera lucida drawings of the setæ in the dorsal and ventral bundles.

The Naididæ are distinguished from the other families of the Oligochæta primarily by the fact that their normal method of reproduction is by means of budding, and that complete intersegmental dissepiments are present. The closely allied family Æolosomatidæ are without dissepiments and are usually of much smaller size. Furthermore, the presence of colored "oil drops" together with the absence of biuncinate setæ are characters which as a rule [1] will serve to distinguish these families. The Enchytræidæ may be separated by the absence of biuncinate setæ, while representatives of the families Lumbriculidæ and Tubificidæ

[1] Colored oil drops are absent in *Æolosoma beddardi*, *Æolosoma niveum* from North America, and two species of Pleurophleps occurring in Ceylon and Central America.

usually exceed 20 mm. in length, while the Naididæ on the contrary are rarely more and usually much less than 15 mm. in length.

The form and position of the setæ are the chief characters relied upon for the separation of the genera and species. These may be long and hair-like (capilliform), short and straight (needle-like), or S-shaped (sigmoid), and may terminate simply or in two hooks (biuncinate). A slight enlargement (nodulus) is usually present on all biuncinate setæ. The accompanying diagrams representing a typical Naid (Fig. 1) together with the different

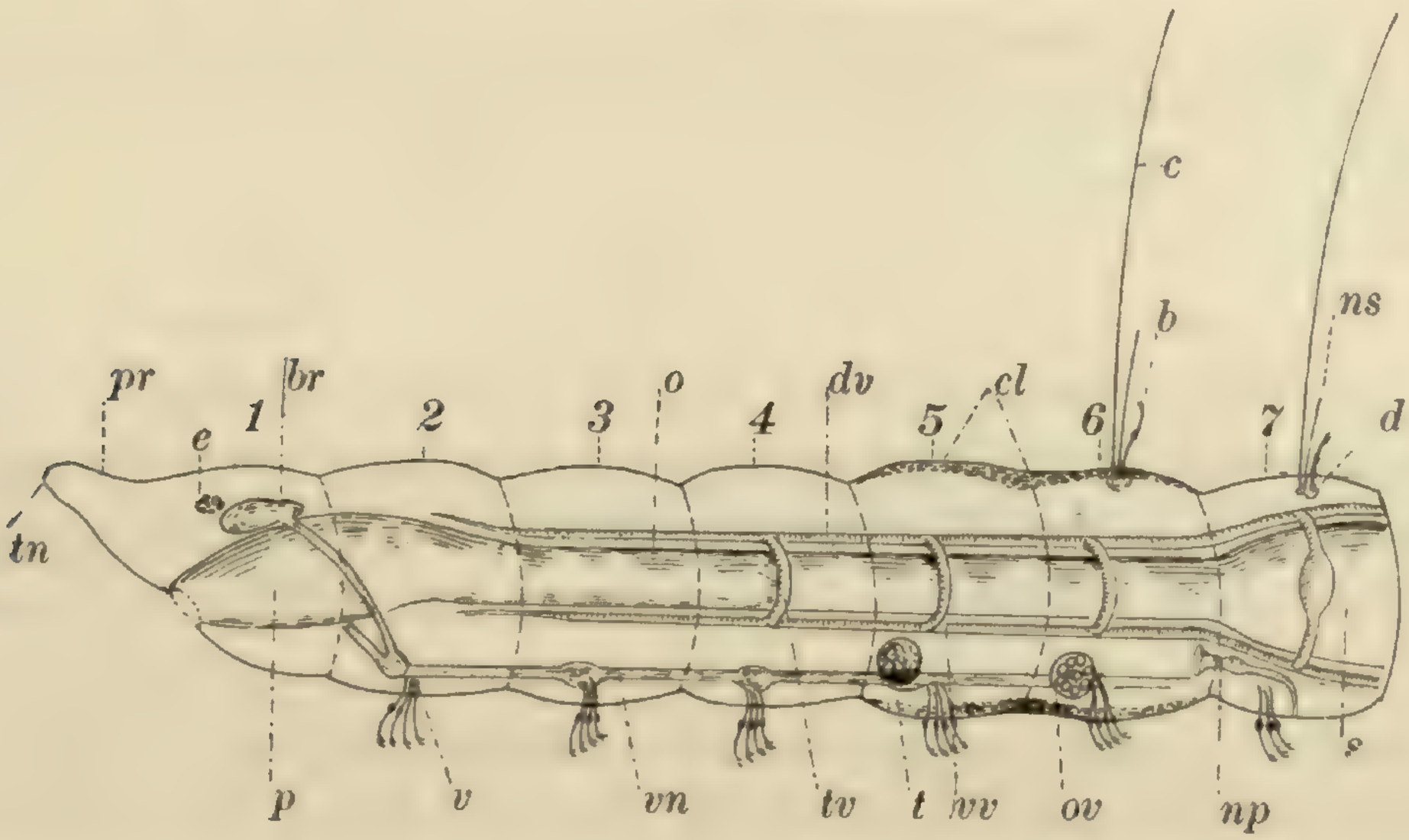

FIG. 1.— Typical Naid illustrating characters used in the tables for separating genera and species. The following abbreviations are used in this and subsequent figures. *b*, biuncinate seta; *br*, brain; *c*, capilliform seta; *cl*, clitellum; *d*, dorsal bundle of setæ: *dp*, digitiform process (see Fig. 5); *dt*, distal tooth, biuncinate seta; *dv*, dorsal blood vessel; *e*, eye; *n*, nodulus; *np*, nephridium; *ns*, needle-like seta; *o*, esophagus; *ov*, ovary; *p*, pharynx; *pr*, prostomium; *ps*, palmate seta; *pt*, proximal tooth, biuncinate seta; *s*, stomach; *sp*, spermatheca; *t*, testis; *tc*, fine teeth on capilliform seta in Pristina; *tc*, prominent teeth on capilliform seta in the genus Vejdovskyella; *tn*, tentacular process; *tp*, tubular respiratory process; *tv*, transverse blood vessel; *v*, ventral bundle of setæ; *vn*, ventral nervous system; *vv*, ventral blood vessel; 1–7, seven anterior segments.

forms of setæ (Fig. 2) will prove of assistance in making clear the characters used in the synoptic table which has been slightly modified from Michaelsen (:00) who in turn adopted a large proportion of it from Vejdovsky ('84). The reproductive organs have not been sufficiently studied to admit of a final conclusion concerning their typical arrangement. This includes all genera known up to the present time, those occurring in North America being

printed in heavier type. Since the publication of this monograph by Michaelsen one new genus (Hæmonais) has been founded by Bretscher, while Michaelsen (:03) has proposed the name Vejdovskyella for Bohemilla, the latter being preoccupied.

FAMILY NAIDIDAE

1791. *Nais* [ex Ord. Mollusca, e Class. Vermes] (part) Gmelin, *Syst. Nat.*, vol. 6, p. 3120.

1895. *Naidomorpha* (e Group *Microdrili*) Beddard, *Monogr. Olig.*, p. 275.

1900. *Naididæ* Michaelsen, *Monogr. Olig.*, *Das Tierreich*, Lief. 10, p. 16.

1903. *Naididæ* Michaelsen, *Die geogr. Verbreit. d. Olig.*, p. 41.

1905. *Naididæ* Michaelsen, "Zur Kenntnis d. Naididen," *Zoölogica*, vol. 18, p. 350.

Setæ aggregated together in 2 or 4 bundles on a segment. Dorsal bundles composed of capilliform, short needle-like, or sigmoid (the latter biuncinate) setæ; dorsal bundles often absent; ventral bundles composed of sigmoid biuncinate setæ. Dissepiments well developed. Brain, commissure, and ventral nerve-cord well developed, distinct from the hypodermis. Esophagus without muscular stomach. Nephridia large, occasionally entirely absent. Testes in segment 5 or 7 (rarely in segments 8 and 9). Ovaries in segments 6 and 7 (rarely in segment 10). Spermatheca in segment 5 or 7. Reproduction normally asexual by budding. Length of specimens varies from 1 to 50 mm.; usually from 2 to 10 mm.

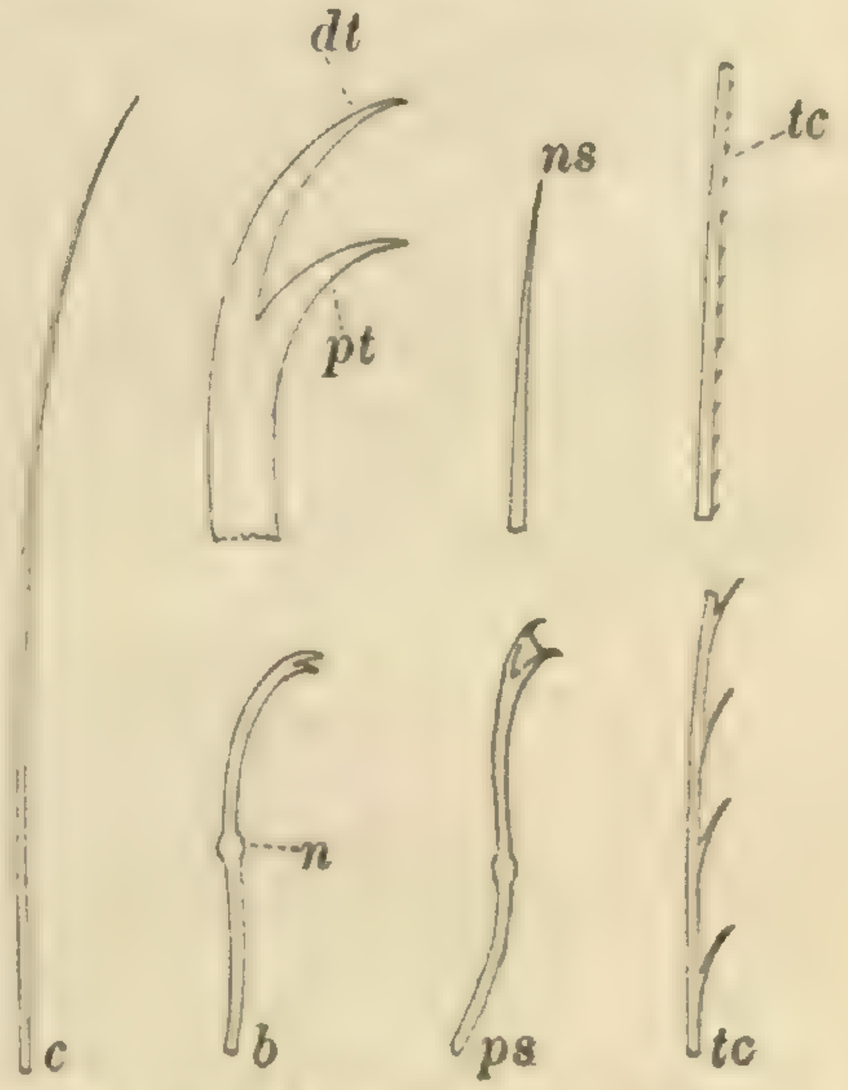

FIG. 2.— Principal types of setæ occurring in the Naididæ. For abbreviations see Fig. 1.

Usually in fresh water, rarely in saline waters. One (Amphichæta) marine. Cosmopolitan; fifteen genera.

Synoptic Table for Separation of Described Genera

(Genera occurring in North America printed in heavy type)

A[1]. Capilliform setæ absent.
B[1]. Dorsal bundles of setæ absent.
C[1]. Ventral bundles of setæ on all segments beginning with the second. Third segment not longer than remaining segments *Schmardella.*
C[2]. Ventral bundles of setæ absent on segment 3–5. Segment 3 extremely long . . . . . **Chætogaster.**
B[2]. 2 dorsal and 2 ventral bundles of setæ on a segment.
C[1]. Segment 3 much longer than remaining segments. Length (of described species) not exceeding 2 mm. . *Amphichæta.*
C[2]. Segment 3 not longer than remaining segments. Length (of described species) equal to or exceeding 5 mm.
D[1]. All setæ of dorsal bundle biuncinate . . . . *Paranais.*
D[2]. Some of the setae of dorsal bundle not biuncinate **Ophidonais.**
A[2]. Capilliform setæ present in the dorsal bundle.
B[1]. Dorsal bundle of setæ beginning on segment 2, 5, or 6.
C[1]. Dorsal bundle of setæ beginning on segment 5 or 6.
D[1]. Posterior end developed into a tubular respiratory process containing paired gills. Usually living in tubes composed of plant fragments, etc. . . . . **Dero.**
D[2]. Posterior end without respiratory processes.
E[1]. Capilliform setæ of dorsal bundle with a series of prominent teeth. Dorsal bundle beginning on segment 5 *Vejdovskyella.*[1]
E[2]. Capilliform setæ without teeth. Dorsal bundle beginning on segment 6.
F[1]. Length of capilliform setæ equal to at least twice the diameter of the body.
G[1]. Capilliform setæ on all segments beginning with 6. Prostomium rounded . . . . . *Macrochætina.*
G[2]. Capilliform setæ only on one (6) or a few (6, 7, 8) segments.
H[1]. Capilliform setæ on segments 6, 7, and 8. Prostomium developed into a tentacular process *Ripistes.*
H[2]. Capilliform setæ only on segment 6. Prostomium not developed into a tentacular process **Slavina.**
F[2]. Length of capilliform setæ shorter or rarely longer than diameter of body.

[1] For Bohemilla, previously used as the generic name for a group of Trilobites by Barrande, (Michaelsen. : 03).

G¹. Prostomium developed into a tentacular process **Stylaria.**

G². Prostomium rounded . . . . . **Nais.**

C². Dorsal bundle of setæ beginning on segment 2.

D¹. Anterior capilliform setæ partly covered by filamentous gills *Branchiodrilus.*

D². No filamentous gills present.

E¹. Dorsal bundle usually composed entirely of capilliform setæ. Prostomium developed into a long tentacular process . . . . . **Pristina.**

E². Dorsal bundle composed in part of biuncinate or of short needle-like setæ. Prostomium rounded or with a short tentacular process . . . . . **Naidium.**

B². Dorsal bundle of setæ beginning on segment 12–20 *Hæmonais.*

Genus CHAETOGASTER K. Baer, 1827

Prostomium rudimentary, coalesced with segment 1; 2 ventral bundles of setæ on a segment, these absent on segments 1 and 3–5. Setæ uncinate. Pharynx large and wide. Esophagus small, not longer than pharynx; 1 pair of transverse vessels connects the dorsal and the ventral vessels. Longitudinal commissures of ventral nerve-cord more or less distinct in anterior part of body. Testes in segment 5, ovaries in segment 6, spermathecæ in segment 5.

In fresh water, free-living or parasitic on fresh-water snails. Middle and south Europe, North America.

Five species are recognized by Michaelsen and to these must be added *C. pellucidus.* Three species of Chætogaster (*C. diastrophus*, *C. diaphanus*, and *C. limnæi*) have been reported from North America, while Leidy ('52), described *C. gulosus*, so incompletely, however, that it cannot be recognized, although undoubtedly referable to the genus Chætogaster.

The following table will serve to separate all the species known at the present time: —

A¹. Prostomium distinct, usually with a pore on anterior margin *C. diastrophus.*
(Europe, N. America.)

A². Prostomium indistinct.

B¹. Length of individuals not exceeding 5 mm.

C¹. Esophagus as long as pharynx.

D¹. Blood vessels of pharyngeal region well developed *C. langi*. (Europe, N. America.)

D². Blood vessels of pharyngeal region absent or only slightly developed . . . . . *C. crystallinus*. (Europe.)

C². Esophagus shorter than pharynx, indistinct.

D¹. Ventral setæ 8 to 12 in bundle, 1st postesophageal dilation of intestine covered with anastomosing network of blood vessels . . . . . *C. limnæi*. (Europe, N. America.)

D². Ventral setæ 6–7 in bundle, 1st postesophageal dilation of intestine surrounded by 12 or more pairs of non-anastomosing transverse blood vessels . . . . . *C. pellucidus*. (N. America.)

B². Length of individuals 10–15 mm. . . . . *C. diaphanus*.

Chætogaster langi Bretscher

C. langi Bretscher, *Rev. Suisse Zoöl.*, vol. 3, p. 512, fig. 1, 1896; Michaelsen, *Das Tierreich, Oligochaeta*, Berlin, p. 21, 1900.

Living specimens transparent. Prostomium blunt, indistinct. Setæ unequally bifid at distal end, 4 in a bundle. Esophagus long. Ventral ganglia glandular in form. Circulatory system with normal development in the pharyngeal region, 1 pair of transverse vessels (not developed as "hearts") in esophageal segment. Length 1–2 mm.

FIG. 3. — *Chætogaster langi* Bretscher (x25). For abbreviations see Fig. 1.

Between filaments of algæ in swampy places, etc.

One specimen (Fig. 3) referable to this species was obtained early in July. There were several minor characteristics not wholly in agreement with the description of *C. langi*, but in the absence of more material it must be placed here.

Chaetogaster pellucidus n. sp.

Transparent. Prostomium indistinct. Eyes absent. Dorsal setæ absent, ventral setæ 6–7 in a bundle, biuncinate, with teeth unequal. Esophagus short, postesophageal dilation (first stomach) sur-

rounded by 12 or more pairs of non-anastomosing transverse blood vessels. Length 1.5 mm. Number of segments in an individual from 9 to 11. Budding in all specimens observed.

Sandusky Bay, Lake Erie.

A considerable number of specimens of this small Chætogaster were observed in cultures of aquatic plants during July and August, and a number were stained and mounted and are now in the

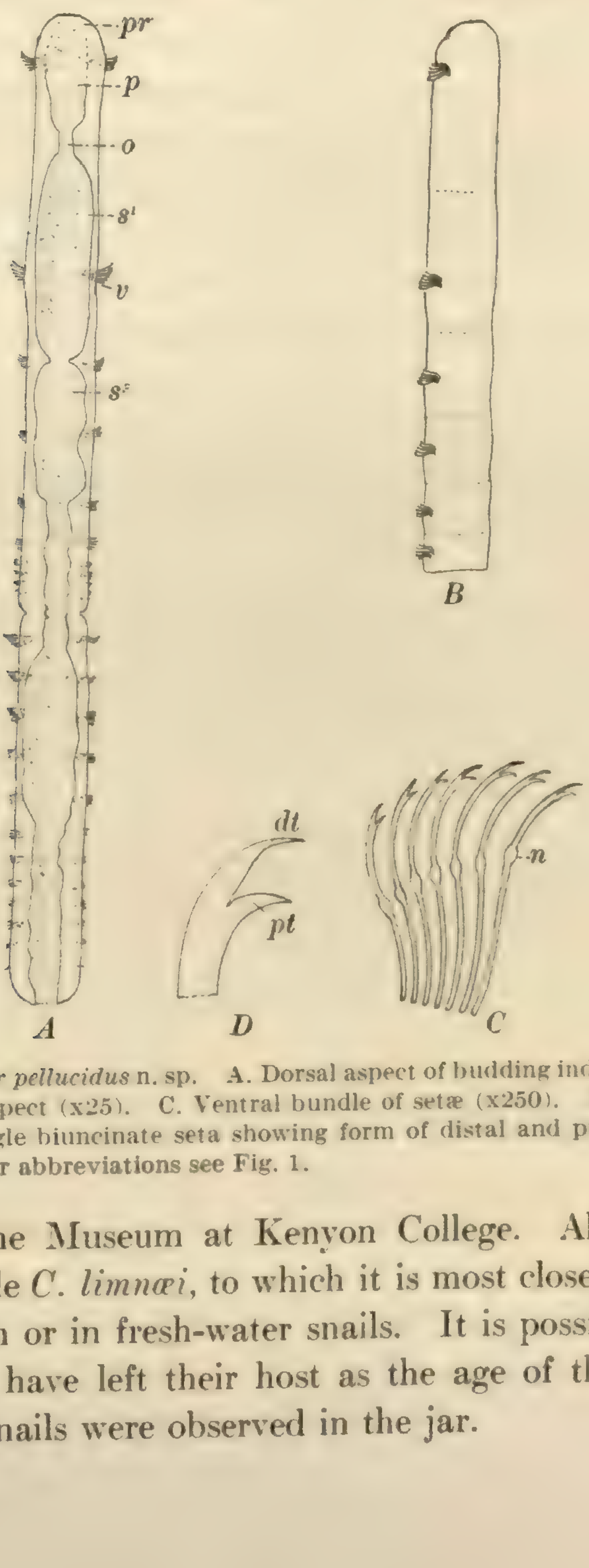

FIG. 4.— *Chætogaster pellucidus* n. sp. A. Dorsal aspect of budding individual (x25). B. Lateral aspect (x25). C. Ventral bundle of setæ (x250). D. Distal portion of a single biuncinate seta showing form of distal and proximal tooth (x1000). For abbreviations see Fig. 1.

collection of the Museum at Kenyon College. All found were free living, while *C. limnæi*, to which it is most closely allied, normally occurs on or in fresh-water snails. It is possible, however, that they may have left their host as the age of the culture increased. No snails were observed in the jar.

Furthermore, Vejdovsky ('84) figures the first postesophageal dilation of *C. limnæi* as being covered with an anastomosing network of blood vessels, while in *C. pellucidus* they are plainly non-anastomosing.

Genus DERO Oken, 1815

Prostomium rounded, eyes absent. Setæ in four bundles on a segment. Ventral setæ uncinate, those of the segments 2 to 5 longer than the rest; dorsal bundle usually beginning on the 6th rarely on the 5th segment, composed of a capilliform and one or two needle-like setæ with variously formed distal ends. Posterior end developed into branchial filaments. Intestine with stomach. Blood red. Nephridia paired from 6th segment. Testes in 5th, ovaries in 6th, spermathecæ in 5th segments.

Fresh water. Europe, North America, Antilles, tropical East Africa, Tonkin, Philippines; fifteen species.

Four species of Dero have been reported from North America: *D. obtusa*, *D. limosa*, *D. vaga*, and *D. furcata*.

Dero vaga (Leidy)

Aulophorus vagus Leidy, *Amer. Nat.*, vol. 14, p. 423, figs. 3, 4, 1880; Reighard, *Proc. Amer. Acad.*, vol. 20, p. 88, pl. 1, figs. 1–10; pl. 2, figs. 11–20; pl. 3, figs. 21–31, 1885.

Dero vaga L. Vaillant, *Hist. Nat. Annel.*, vol. 3, p. 383, 1890; Stieren, *Sitzb. Ges. Dorpat*, vol. 10, p. 107, 1893.

D. furcata Bousfield (part), *Journ. Linn. Soc. London*, vol. 20, p. 105, 1887.

D. vaga Michaelsen, *Das Tierreich, Oligochæta*, p. 29, 1900.

Prostomium rounded. Ventral bundle of segments 2 to 5 with 8 to 14 long slightly curved, biuncinate setæ, with upper somewhat longer than the lower tooth. Ventral bundles of remaining segments with 4 to 7 shorter, more curved, biuncinate setæ with the upper shorter than the lower tooth. Dorsal bundle of setæ beginning on 6th segment; composed of 1 to 3 capilliform and 1 to 3 palmate setæ.

Posterior end with rudimentary branchia and two long finger-

like processes. Three pairs of hearts in segments 8, 9, and 10. Brain wider than long. Length 8 mm. or more; number of segments in an individual 24 to 35.

In slime of ditches, etc., among fresh-water plants. Massachusetts (Cambridge), Pennsylvania (Philadelphia), Illinois, Ohio (Cedar Point), and Trinidad, West Indies.

This species was extremely common at Cedar Point, particularly among cultures containing *Riccia fluitans*, the thallus of which together with statoblasts of Bryozoa, etc., it uses in the building of a protective tube by means of a viscid secretion from the body. When walking around with its tube it bears a striking resemblance to a minute caddis-fly larva.

Genus STYLARIA Lamarck, 1816

Prostomium developed into a tentacular process. Ventral bundles composed of biuncinate setæ; dorsal bundle composed of capilliform setæ, beginning on 6th segment. Testes in 5th, ovaries in 6th, spermathecæ in 5th segment.

Fresh water. Europe, North America; one species.

Stylaria lacustris (Linné)

Nereis lacustris Linné, *Syst. Nat.*, ed. 10, p. 654, 1758; ed. 12, vol. 2, p. 1085, 1767.

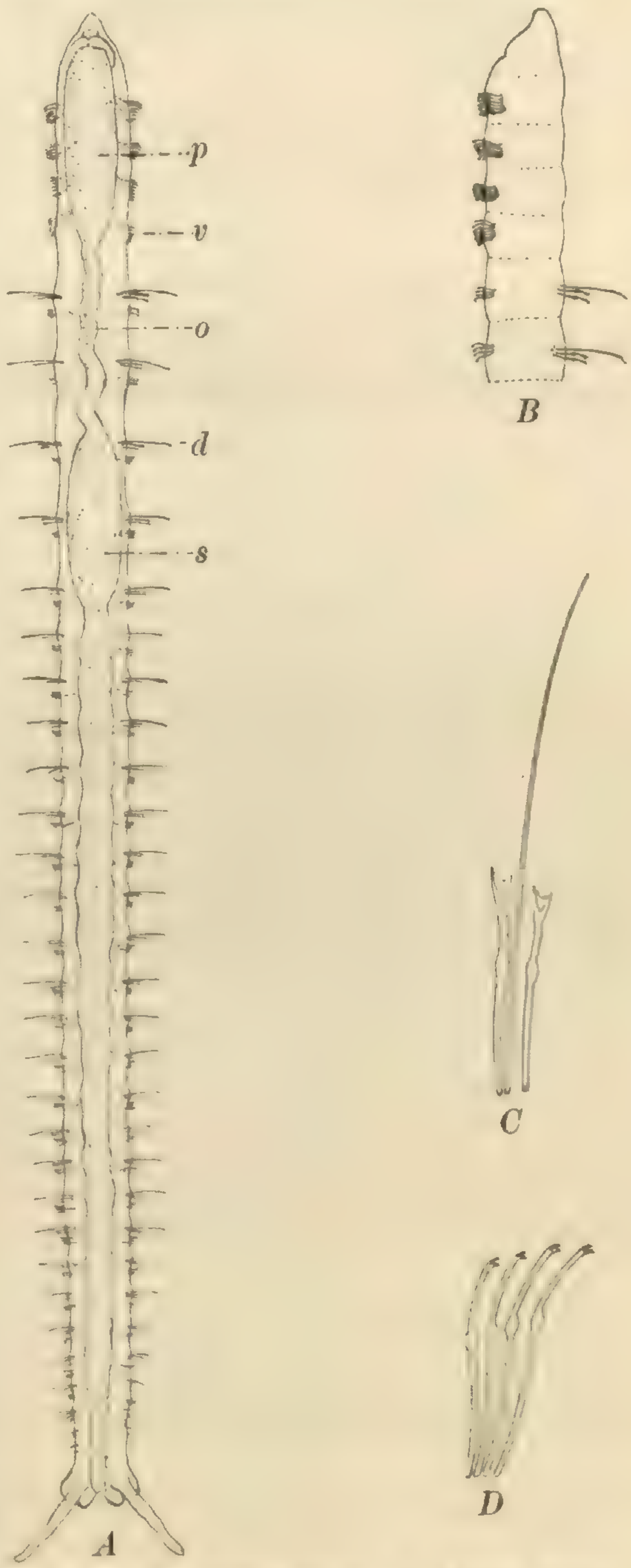

FIG. 5.— *Dero vaga* Leidy. A. Dorsal aspect (x25). B. Lateral aspect, first six segments (x25). C. Dorsal bundle of setæ (x250). D. Ventral bundle of setæ, 6th segment (x 250). For abbreviations see Fig. 1.

Stylaria lacustris Johnston, *Cat. Brit. Non-paras. Worms*, p. 70, 1865; Vejdovsky, *Syst. Morphol. Olig.*, p. 30, pl. 3, fig. 27; pl. 4, figs. 1–24, 26–31, 1884.

Nais lacustris Beddard, *Monogr. Olig.*, p. 284, 1895; Michaelsen, *Das Tierreich, Oligochæta*, p. 33, 1900.

S. paludosa, S. fossularis Leidy, *Proc. Acad. Nat. Sci. Phila.*, vol. 5, pp. 286, 287, 1852.

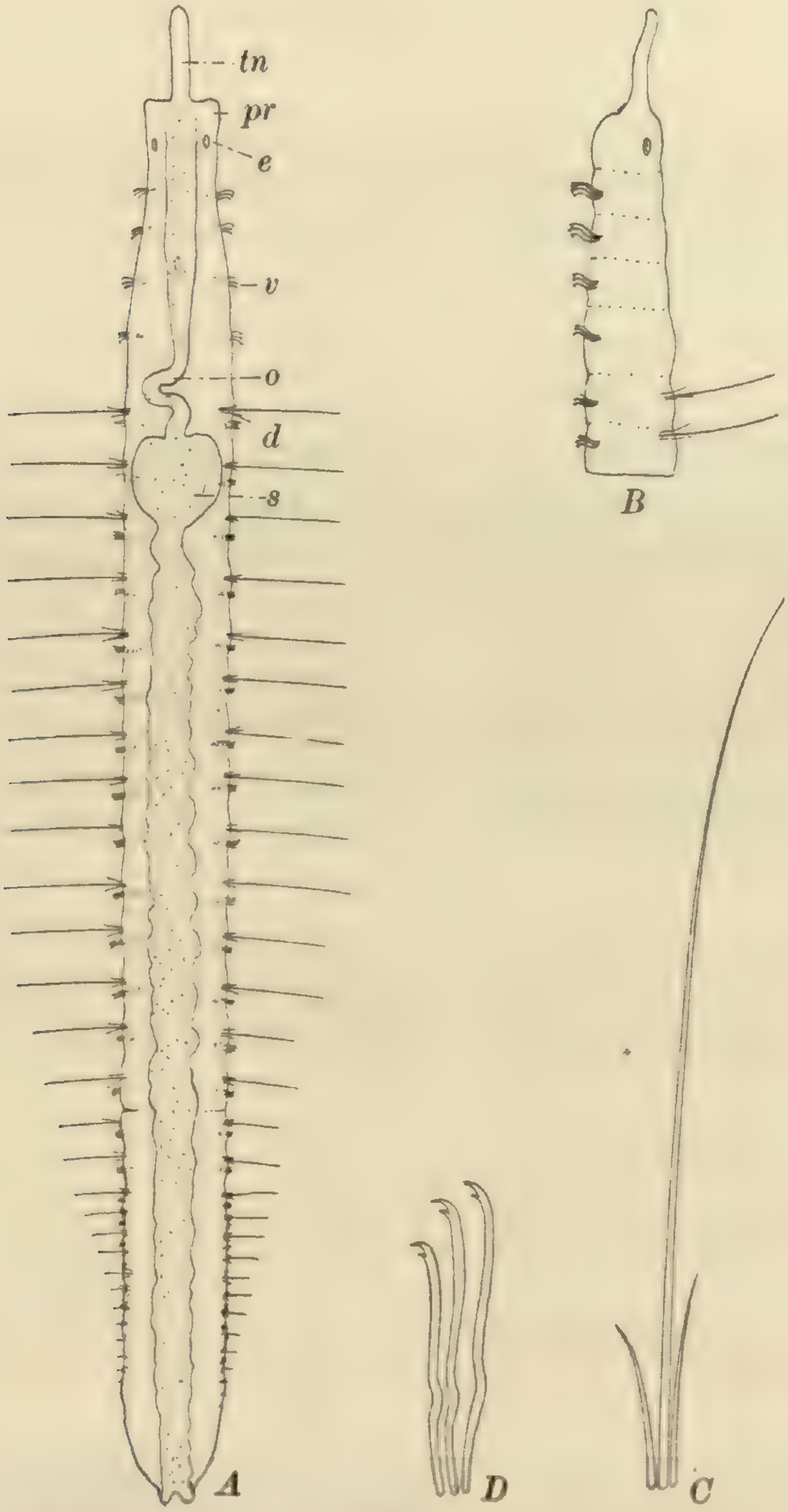

FIG. 6.— *Stylaria lacustris* (Linné). A. Dorsal aspect (x25). B. Lateral aspect, first 6 segments (x25). C. Dorsal bundle of setæ of 6th segment (x250). D. Ventral bundle of setæ, 4th segment (x250). For abbreviations see Fig. 1.

S. phyladelphiana, S. scotica Czerniavsky, *Bull. Soc. Imp. Nat. Moscou,* vol. 55, no. 4, p. 309, 1880.

Prostomium developed into a long tentacular process. Eyes usually present. Distal teeth of ventral setæ unequal. Dorsal setæ capilliform with 1 long and 1 to 2 short in each bundle. All long setæ of each bundle approximately of the same length. Clitellum in sexually mature forms on segment 6. Male pores on 6th segment. Sperm duct in 5th, spermathecæ in 5th segment. Length 10 to 15 mm. Number of segments about 25.

Europe, North America (Pennsylvania, Ohio, Illinois).

A large number of specimens were observed which must at present be referred to this species. Michaelsen notes the length of *N. lacustris* as varying between 10 and 15 mm., while the length of those found at Cedar Point was always from 4 to 5 mm. The teeth of the ventral setæ are also considerably shorter and more obtuse than illustrated in the figures of Vedjovsky ('84), Tauber, and others. Furthermore, the length of the tentacular process in those forms observed, did not exceed the length of the long capilliform setæ while Müller (1774) notes the length of the tentacular process as equivalent to ten segments of the body. The synonymy of *S. lacustris* is in a confused condition, and it is possible that careful study will establish one or more new species in the genus.

The imperfect descriptions given by Leidy ('52b) to the species described by him as *S. paludosa* and *S. fossularis*, will not permit their separation from *S. lacustris.*

Genus Nais Müller, 1774

Prostomium rounded. Ventral bundle with biuncinate setæ. Dorsal bundle beginning on the 6th segment with capilliform and variously pointed short setæ. Testes in 5th, ovaries in 6th, spermathecæ in 5th segments (in species where sex organs have been observed).

In fresh water. Europe, North America, South America, and East India; ten species.

The genus Nais furnishes one of the most difficult problems for the systematist attempting to define the limits of species among

the Naididæ. The following table, however, embodies the results of systematic work so far as they are known and comprises all species described up to the present time.

A[1]. Setæ of ventral bundle of segments 8 to 10 neither thicker than those of other segments nor modified by possessing blunt tips with rudimentary lower tooth.

B[1]. Eyes present.

C[1]. Ventral setæ of segments 2 to 5 much longer than those of succeeding segments. Dorsal setæ capilliform, 4 to 8 in bundle *N. obtusa.*
(Europe, S. Siberia.)

C[2]. Ventral setæ of segments 2 to 5 not decidedly longer than those of succeeding segments.

D[1]. Transverse blood vessels simple.

E[1]. Ventral setæ of segments 2 to 5 unequally bifid at tip. Length 1 to 1.5 mm. . . . . *N. elinguis.*
(Europe, N. America, S. America.)

E[2]. Ventral setæ of segments 2 to 5 equally bifid at tip.

F[1]. Number of segments in an individual approximately 10 (9 to 10), 6 to 8 ventral setæ in a bundle. Length of specimen 1.5 mm. . . . . *N. parvula.*
(N. America.)

F[2]. Number of segments in an individual usually 20 (18 to 22), 4 ventral setæ in a bundle. Length of specimens at least 2 mm.

G[1]. Dorsal bundles composed of 1 long capilliform and 2 short needle-like setæ. Eyes dumbbell-like in form *N. tortuosa.*
(N. America.)

G[2]. Dorsal bundle composed of 1 long capilliform and 1 short biuncinate seta. Eyes oval, not dumbbell-like in form. Length 3.5 mm. . . . . *N. parviseta.*
(N. America.)

D[2]. Transverse blood vessels of segments 2 to 5 forked. Dorsal bundle with biuncinate setæ. . . . . *N. heterochæta.*
(England.)

B[2]. Eyes absent.

C[1]. Proximal tooth of dorsal biuncinate setæ not longer than the distal tooth.

D[1]. Ventral bundle composed of 3 to 4 setæ. Length of individuals 3 to 3.5 mm. Colorless . . . *N. tenuidentis.*

D[2]. Ventral bundle composed of 6 to 8 setæ. Length 6 to 8 mm. Color reddish . . . . . *N. josinæ.*
(Europe, N. America.)

C². Proximal tooth of dorsal biuncinate setæ twice the length and twice the thickness of the distal tooth . . *N. paraguayensis.* (S. America.)

A². Setæ of ventral bundle of segments 8 to 10 much thicker than those of other segments, 1 to 2 in number, tips blunt, proximal tooth rudimentary . . . . . *N. bretscheri.* (Europe.)

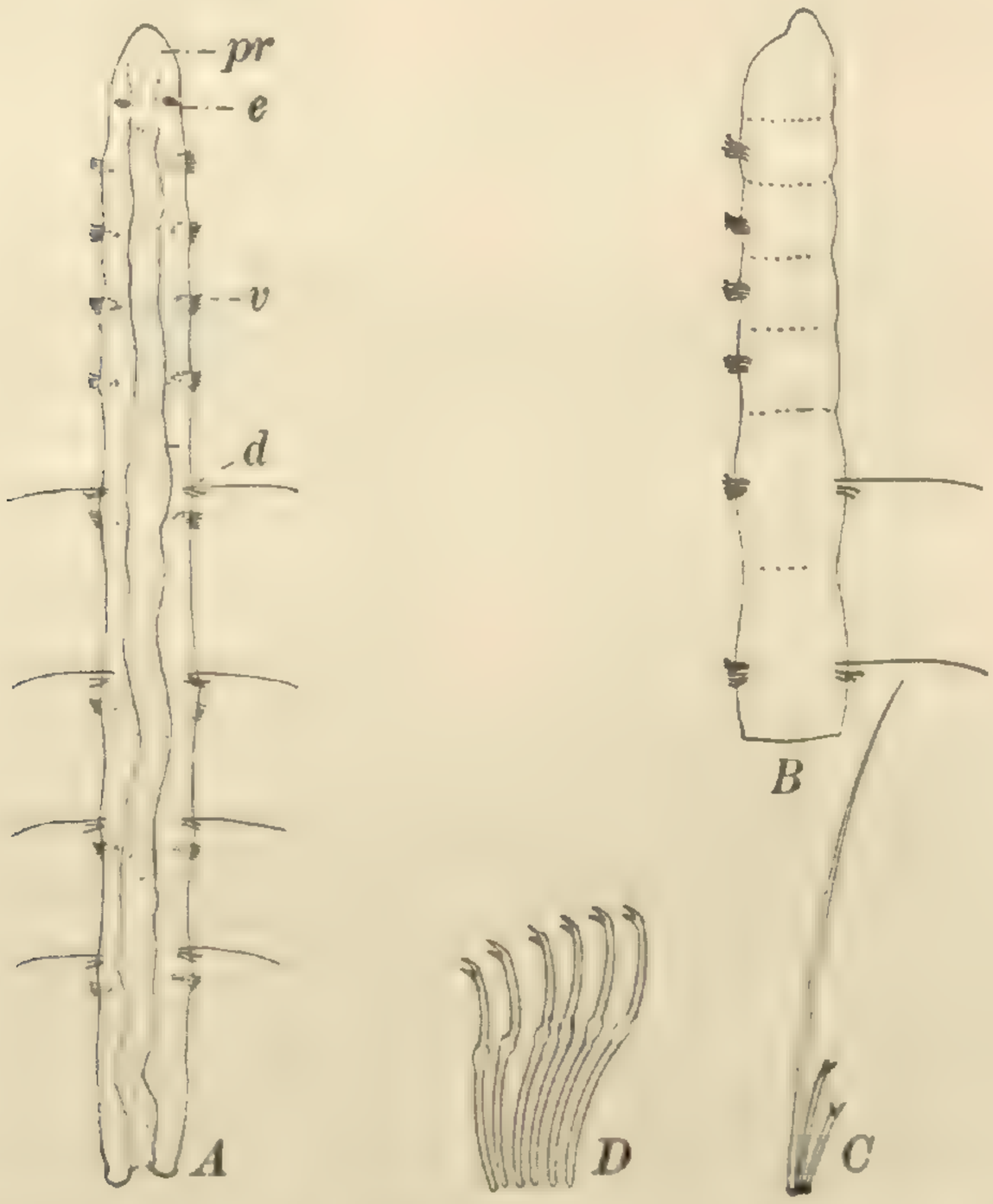

FIG. 7.— *Nais parvula* n. sp. A. Dorsal aspect (x50). B. Lateral aspect, first six segments (x50). C. Dorsal bundle of setæ of 6th segment (x250). D. Ventral bundle of setæ, 6th segment (x250). For abbreviations see Fig. 1.

Nais parvula n. sp.

Prostomium blunt, rounded. Eyes present. Digestive tract not differentiated into esophagus and stomach. Dorsal bundle beginning on segment 6, composed of 1 capilliform, subequal to diameter of body, and 2 short biuncinate setæ. Ventral bundle consisting of 6 to 7 biuncinate setæ with teeth equal. Length 1.2 mm. Number of segments in an individual 9 to 10.

Cedar Point, Sandusky, Ohio.

Several examples of this extremely small Nais were found in the slime accumulating at the bottom of jars containing roots of various aquatic plants obtained from Sandusky Bay. It is chiefly

remarkable by reason of its small size, and the limited number of segments composing the body. At first it seemed probable that it was an immature form but evidence to the contrary was given by budding in several specimens.

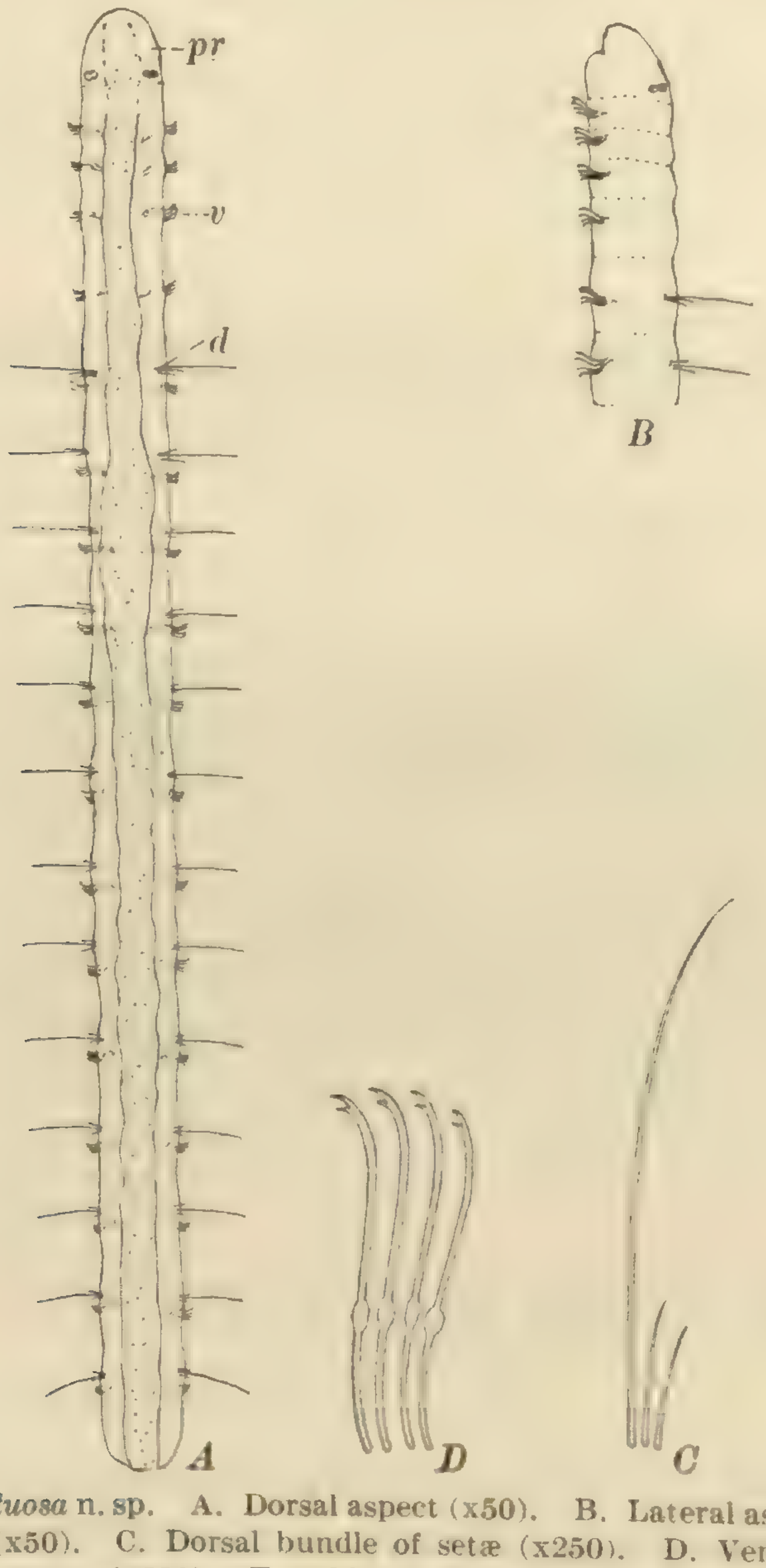

FIG. 8.— *Nais tortuosa* n. sp. A. Dorsal aspect (x50). B. Lateral aspect of first six segments (x50). C. Dorsal bundle of setæ (x250). D. Ventral bundle of setæ, 2d segment (x250). For abbreviations see Fig. 1.

Nais tortuosa n. sp.

Prostomium blunt, rounded. Eyes present slightly dumbbell-shaped. Digestive tract not differentiated into esophagus nor stomach. Dorsal bundle beginning on 6th segment, composed of 1 long capilliform (180 μ) and 2 short (50 μ) needle-like setæ. Ven-

tral bundle consisting of 4 biuncinate setæ (110 μ) with subequal teeth. Length 2.2 mm. Number of segments in an individual 18.

Cedar Point, Sandusky, Ohio.

Two specimens belonging to this species were noted. Budding was not observed. Several Peritrichous ciliates (*Rhabdostyla* sp., length 50 μ, diameter 19 μ) were observed fixed to the anterior end of one of the individuals, the peduncle being less than 2 μ in length.

Nais parviseta n. sp.

Prostomium narrow, slightly acute. Eyes present, round or slightly oval. Digestive tract differentiated into a distinct pharynx which gradually merges into an esophagus. Stomach dilation scarcely perceptible. Dorsal bundle beginning on the 6th segment, composed of 1 capilliform, subequal to diameter of body, and 1 short biuncinate seta, possessing equally developed teeth and an indistinct nodulus. Ventral bundle composed of 3 to 4 biuncinate setæ, with lower tooth considerably larger than the upper tooth. Length 3.5 mm. Number of segments in an individual 19 to 20.

Cedar Point, Sandusky, Ohio.

A very few specimens of this form were observed. Budding was noted in nearly all of the individuals examined. The characteristic differentiation of the teeth on the ventral setæ appears to be of considerable specific importance.

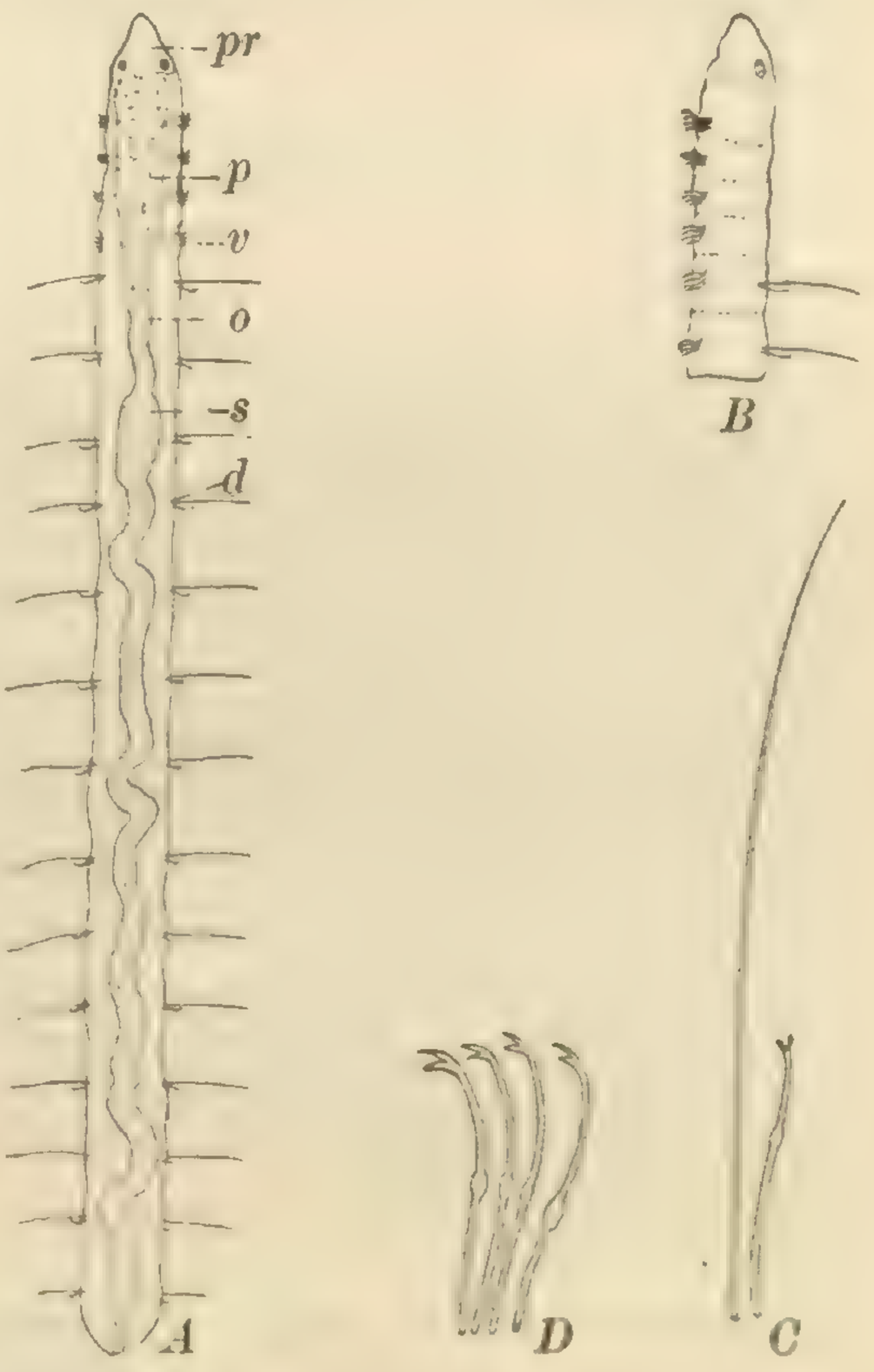

FIG. 9.— *Nais parviseta* n. sp. A. Dorsal aspect (x25). B. Lateral aspect, first six segments (x25). C. Dorsal bundle of setæ (x250). D. Ventral bundle of setæ, 4th segment (x250). For abbreviations see Fig. 1.

Nais tenuidentis n. sp.

Prostomium blunt. Eyes absent. Digestive tract not differentiated into esophagus or stomach, covered with many brownish globules. Dorsal bundle beginning on 6th segment, composed of 1 capilliform, the length (180 μ) of which is approximately one half the diameter of the body, and 1 short (60 μ) biuncinate seta possessing equally developed teeth and provided with a nodulus. Ventral bundle consisting of 4 (3 in several anterior bundles) deeply bifid setæ, both teeth being exceedingly long and slender, the upper measuring 20 μ and the lower 14 μ from the base of the cleft area. Length 3 to 3.5 mm. Number of segments in an individual approximately 20. Budding observed.

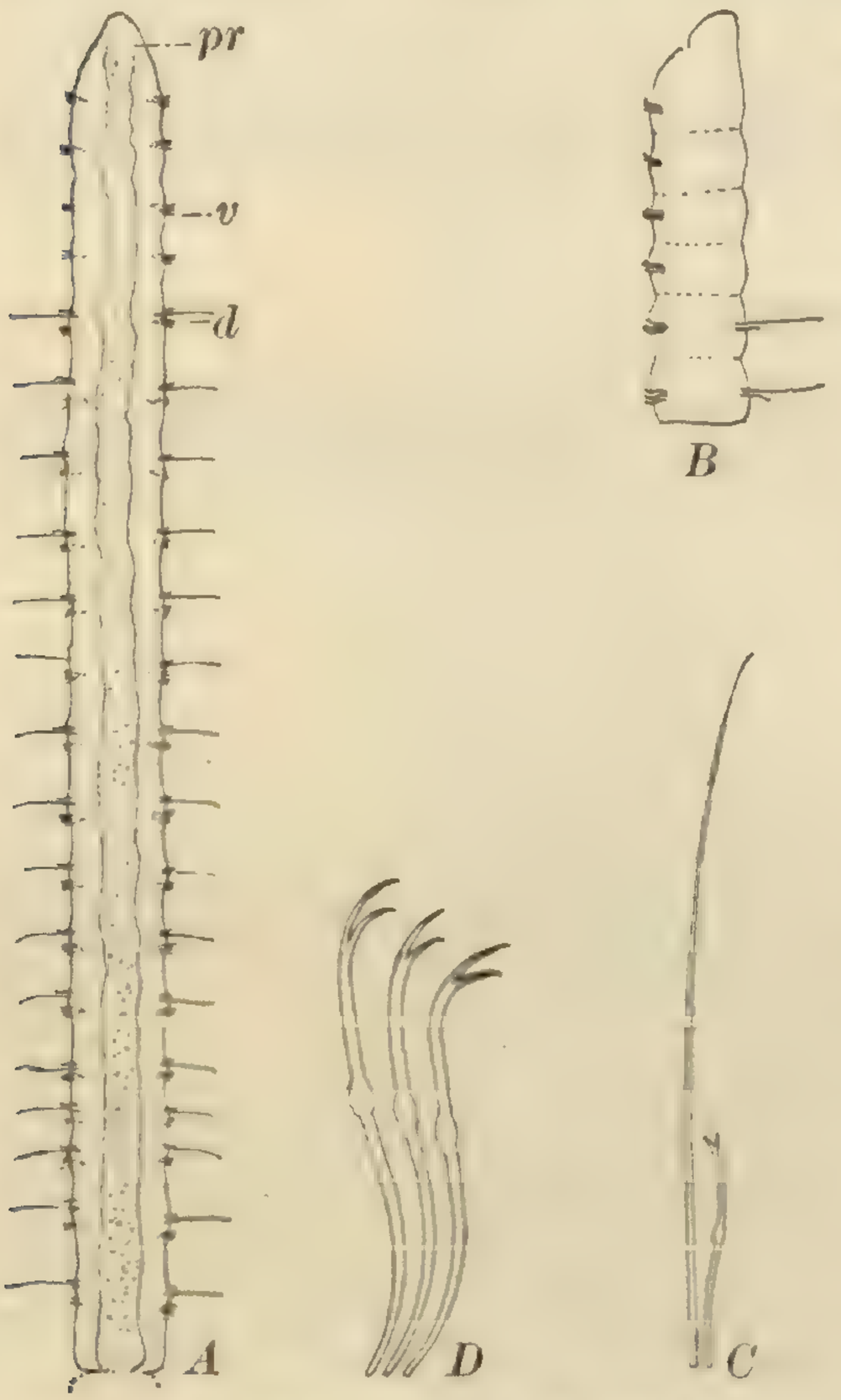

FIG. 10.— *Nais tenuidentis* n. sp. A. Dorsal aspect (x25). B. Lateral aspect, first six segments (x25). C. Dorsal bundle of setæ of 7th segment (x250). D. Ventral bundle of setæ, 2d segment (x250). For abbreviations see Fig. 1.

Cedar Point, Sandusky Ohio.

Only two specimens of *N. tenuidentis* were found, budding occurring in each. The extremely long and slender teeth of the ventral setæ are a striking characteristic of this species.

Genus PRISTINA Ehrenberg, 1831

Prostomium usually developed into a tentacular process. Ventral bundle composed of biuncinate setæ. Dorsal bundle beginning on the 2d segment, composed of capilliform setæ. Testes in 7th, ovaries in 8th, spermathecæ in 7th segments (description of sexual organs based on observation of one species, *P. leidyi*).

In fresh water. Europe, North America, South America, and Java; 6 species.

The species may be separated by the following table. While it is possible that a careful study of *P. æquiseta*, *P. longiseta*, and *P. flagellum*, may show that those responsible for the descriptions have overlooked the existence of the small teeth present in *P. leidyi* and *P. serpentina*, it appears evident that the species are distinct on other grounds.

A[1]. Setæ of dorsal bundle smooth.
  B[1]. Last segment not provided with finger-like processes.
    C[1]. Dorsal setæ of 3d segment not decidedly longer than those of other segments; length 7 to 8 mm. . . . . *P. æquiseta.* (Europe.)
    C[2]. Dorsal setæ of 3d segment much longer than those of other segments . . . . . *P. longiseta.* (Europe.)
  B[2]. Last segment provided with 3 (2 lateral and 1 median) finger-like processes projecting posteriorly . . . . . *P. flagellum.* (N. America, S. America.)

A[2]. Setæ of dorsal bundle provided with numerous fine but distinct teeth.
  B[1]. Capilliform setæ of dorsal bundle approximately 35 μ long. Those of the 3d segment twice as long as the others . . *P. leidyi.* (N. America, S. America.)
  B[2]. Capilliform setæ of dorsal bundle approximately 300 μ long. Those of the 3d segment not longer than others.
    C[1]. Teeth of ventral setæ subequal. Number of segments approximately 14 . . . . . *P. serpentina.* (N. America.)
    C[2]. Distal teeth of ventral setæ longer than proximal teeth. Number of segments 18 to 30 . . . . . *P. proboscidea.* (S. America.)

Pristina serpentina n. sp.

Prostomium developed into a long tentacular process, usually 0.2 to 0.3 mm. in length. Eyes absent. Digestive tract with stomach in the anterior part of the 8th segment. Dorsal bundle beginning on the 6th segment, composed of 2 long (300 μ), 1 medium (100 μ) capilliform setæ, and 2 to 6 short needle-like (30 μ to 50 μ) setæ. Ventral bundle composed of 5 to 6 biuncinate (60 μ to 80 μ) setæ with subequal teeth. Length 2.2 mm. Number of segments in an individual about 15.

Cedar Point, Sandusky, Ohio.

This species of Pristina (Fig. 11) was exceedingly abundant at Cedar Point, and on first examination was apparently to be placed near *P. æquiseta* Bourne. Closer examination, however, dem-

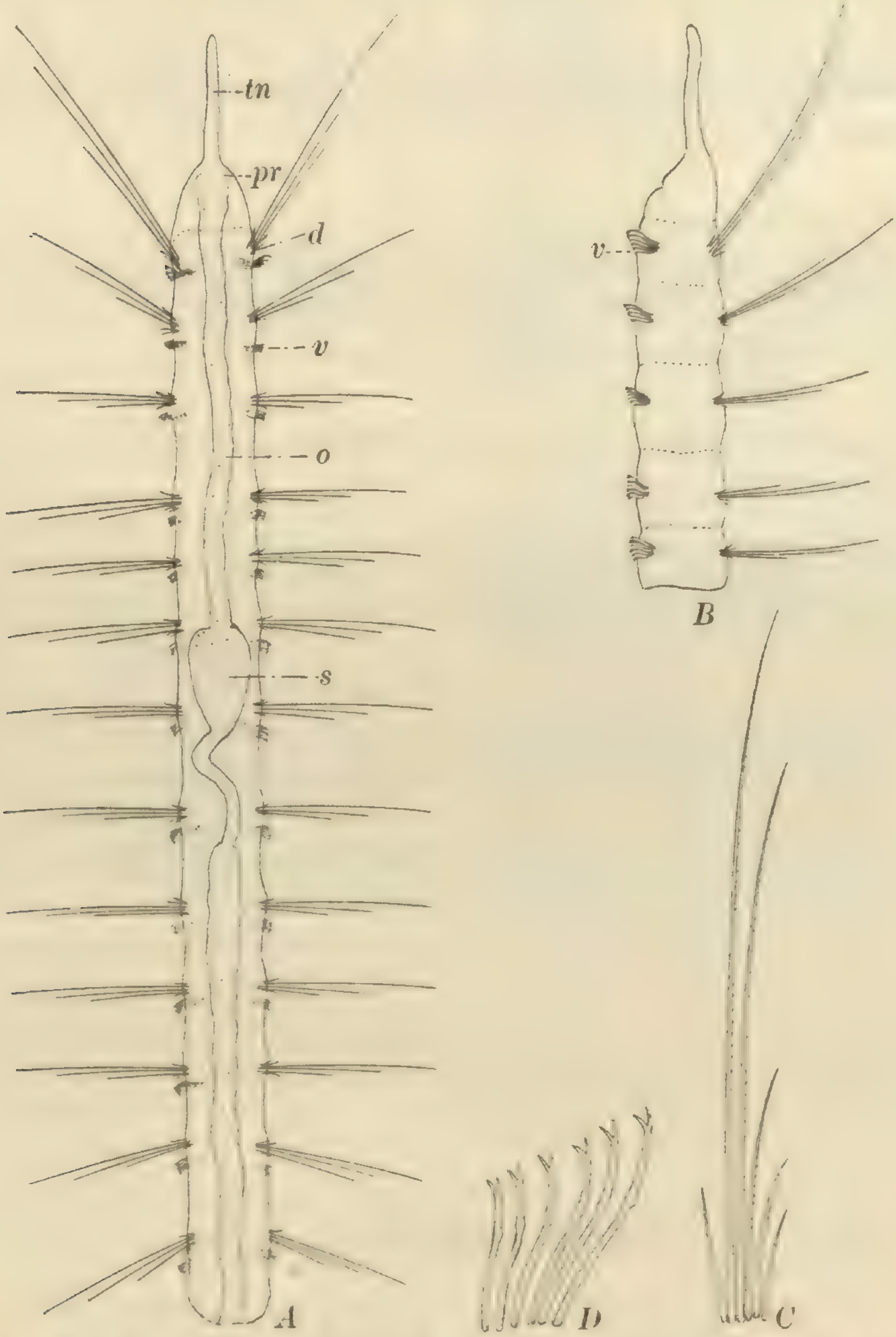

FIG. 11.— *Pristina serpentina* n. sp. A. Dorsal aspect (x50). B. Lateral aspect, first six segments (x50). C. Dorsal bundle of setæ of 7th segment (x250). D. Ventral bundle of setæ (x250). For abbreviations see Fig. 1.

onstrated the existence of fine teeth on the setæ of the dorsal bundle. The difference in the form of the distal teeth of the ventral setæ distinguishes it from *P. proboscidea* Beddard, now recognized by Michaelsen (:05) as a valid species.

Genus Naidium O. Schmidt, 1847

Prostomium either rounded, pointed, or developed into a short tentacular process. Dorsal bundle beginning on the 2d segment, composed of capilliform, or needle-like, and biuncinate setæ. Ventral bundle composed of biuncinate setæ.

Fresh water. Middle Europe, East India, North America, and South America; six species.

A¹. Prostomium not developed into a tentacular process.
  B¹. Number of segments composing an individual usually 15 to 30 (32 to 40, *N. luteum*). Biuncinate setæ in dorsal bundle.
    C¹. Prostomium rounded or pointed, species small, not exceeding 5 mm. in length.
      D¹. Number of segments in an individual 20, posterior part of brain developed into 4 pronounced lobes . *N. bilobatum*. (Europe.)
      D². Number of segments in an individual 15 to 16.
        E¹. Capilliform setæ shorter than the diameter of the body. Teeth of dorsal biuncinate setæ approximate *N. uniseta*. (Europe.)
        E². Capilliform setæ longer than the diameter of the body. Teeth of dorsal biuncinate setæ remote . . *N. osborni*. (N. America.)
    C². Prostomium slightly elongate, species large, approximately 15 mm. in length . . . . . *N. luteum*. (Europe.)
  B². Number of segments in an individual 40 to 61, no biuncinate setæ in dorsal bundle . . . . . *N. dadayi*. (S. America.)
A². Prostomium developed into a short tentacular process, length of species approximating 8 mm. . . . . *N. breviseta*. (East India.)

Naidium osborni n. sp.

Prostomium moderately long, somewhat pointed. Eyes absent. Digestive system differentiated into pharynx (segments 1 to 3), esophagus (segments 4 to 7), and stomach (8th segment). Dorsal bundle of setæ beginning on the 2d segment, composed of 1 long capilliform (145 μ) and 1 short (50 μ) seta, the latter biuncinate

with subequal, remote teeth and an indistinct nodulus one third the distance from the tip. Ventral bundle composed of 4 biuncinate setæ with subequal teeth and a distinct nodulus midway between base and tip. Length 1.6 mm. Number of segments in an individual 15 to 16. Budding observed.

Cedar Point, Sandusky, Ohio.

Five species of Naidium have been described: three from central Europe, one from the East Indies, and one from South America; none, however, has been noted in North America, consequently the occurrence of a distinct species in the United States is of considerable interest. A single individual was found in the sediment of a bottle containing "reed roots" obtained at Cedar Point, Ohio, and received from Professor Osborn, September 4, 1905.

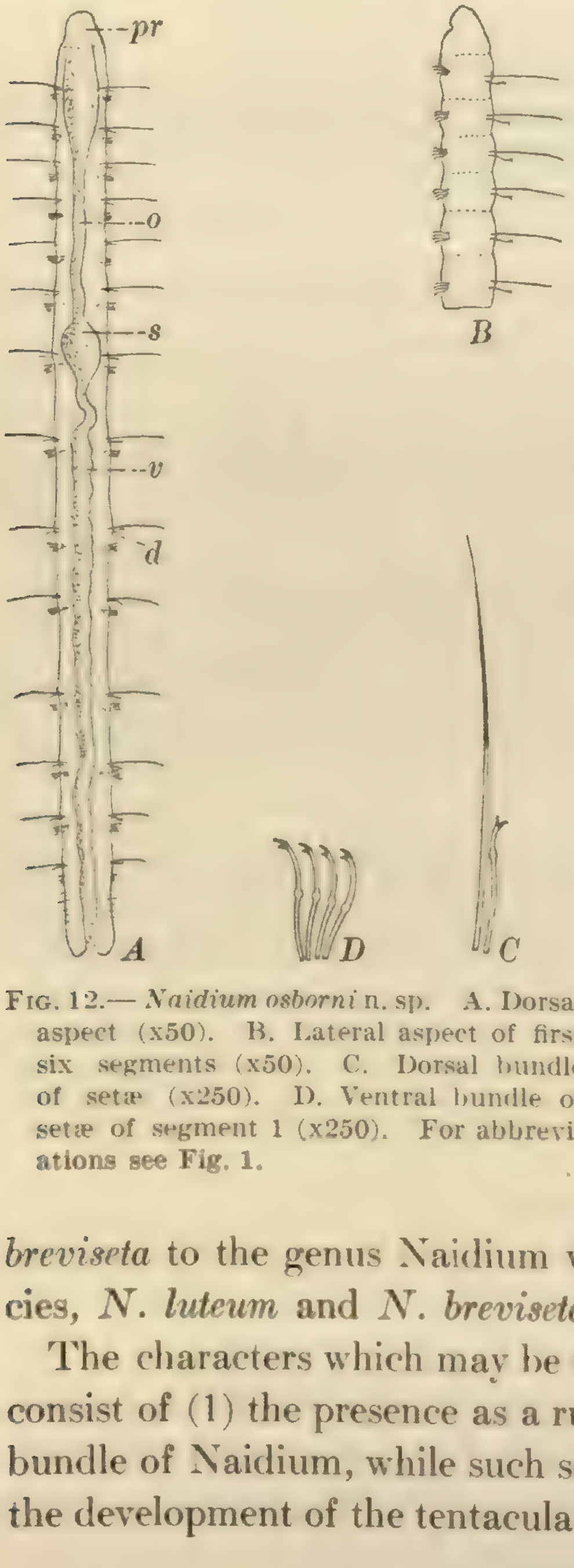

FIG. 12.— *Naidium osborni* n. sp. A. Dorsal aspect (x50). B. Lateral aspect of first six segments (x50). C. Dorsal bundle of setæ (x250). D. Ventral bundle of setæ of segment 1 (x250). For abbreviations see Fig. 1.

Schmidt (1847) founded the genus upon a single species, *N. luteum*, occurring in Europe. Beddard ('95) maintained that this species should be incorporated in the genus Pristina inasmuch as *Pristina breviseta* described by Bourne (1891) nearly bridged over the gap formerly supposed to separate the two genera. Michaelsen (:00) removed *P. breviseta* to the genus Naidium which thus consisted of two species, *N. luteum* and *N. breviseta*.

The characters which may be used for separating the two genera consist of (1) the presence as a rule of biuncinate setæ in the dorsal bundle of Naidium, while such setæ are absent in Pristina, and (2) the development of the tentacular process of the prostomium which

is either absent or extremely short in Naidium while in Pristina it is long. The absence of any tentacular process in *N. osborni* suggests that until a species is found in which the process is well developed and in which the dorsal bundles contain biuncinate setæ, the genera may be considered distinct. Further studies may show other generic characters.

I take pleasure in dedicating this species to Professor Herbert Osborn, Director of the Lake Laboratory, Sandusky, Ohio.

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MECHANISM OF THE ODONTOPHORAL APPARATUS IN *SYCOTYPUS CANALICULATUS*

J. C. HERRICK

Introduction

This paper gives the results of some four or five weeks spent in dissecting and experimenting on the odontophoral apparatus in the large familiar whelk or winkle, *Sycotypus canaliculatus* (Linn.).[1] The work was done at the Marine Laboratory at Wood's Hole, Mass., during the summer of 1905. I desire to express here my thanks to the direction of the laboratory for the material furnished and privileges extended, especially to Dr. G. A. Drew to whom I am indebted for advice and encouragement.

The object of the paper is to show the *modus operandi* of the whole odontophoral mechanism as found in the form selected, and also, incidentally to describe the nervous supply of the muscles that control the mechanism. To this end the anatomy of the parts has to be described in some detail, but it is hoped that the figures which accompany the text may serve to give some substance to the descriptions.

Sycotypus because of its large size offers excellent material for such a study. The whole apparatus can be studied with the naked eye, no dissecting lens being necessary except for examining the teeth. Besides, since this animal is a great pest to the oysterman and clam digger on account of its depredations upon the beds, it is of some interest — aside from the purely scientific — to know more intimately how this gastropod accomplishes its destructive work of boring through the shells of oysters and clams, and rasping out their soft contents by means of its file-like "tongue."

[1] Synonymy (Verrill): Murex, Pyrula, Busycon, Fulgur.

METHOD

The method followed was that of gross dissection, combined with that of stimulation by the induced electric current, of the muscles and nerves concerned. The animals were freed from their shells by means of a hatchet, chipping away the shell along the line of the canal, and finally twisting the animal out; and then left for twelve hours or more in a mixture of waste alcohol and turpentine. This treatment [1] causes the animal to put forth its proboscis usually in full extension, and does not really kill it, though, of course, causing deep narcosis. In this condition the various muscles (or nerves) can be dissected out, stimulated, and their action studied.

HISTORICAL

Huxley, in 1853, was the first to study the mechanism of the buccal or odontophoral apparatus in a number of forms. He observed it in action in the transparent heteropod, Firoloides, and from what he saw was led to believe that Cuvier had failed to grasp the mode of operation of the same apparatus which he had described in Buccinum. Cuvier, to quote Huxley, "considered the tongue-plate [radula] to be passive, and that its movements depended upon the protraction, retraction, divergence, or approximation of the cartilages." According to Huxley, Middendorf also, in his elaborate monograph upon Chiton, in which he gives a very careful and detailed description of the buccal apparatus, "fails in rendering its action clear." The radula "acts as a sort of elastic file pushed from behind [!] by a special muscle, the 'curvator radulæ,' and supported and steadied by the 'folliculi motores' [buccal cartilages]."

It will be well to quote in full Huxley's own explanation of the mode of operation of the apparatus, as I deem it the correct one, though, as we shall see, denied subsequently by his pupil, Professor Geddes and others: "I have already described the manner in which the apparatus may be seen working in Firoloides and Atlanta and I propose now to demonstrate that from the anatomical arrange-

[1] Due to Mr. G. M. Gray, Curator, I believe.

ments the 'tongue' has the same chainsaw-like mode of operation throughout the Cephalopoda and Gasteropoda. Perhaps Patella may be taken as the most convenient illustration, since the organ is here very large [however, not nearly so large as in Sycotypus], and its parts are distinct and well developed." After describing the apparatus in Patella, he says: "It is clear that the action of the intrinsic muscular bands (having the insertions described) must be to cause the elastic plate [radular membrane], and with it the 'dentigerous plate' [radula], to traverse over the ends of the cartilages, just like a band over its pulley, the cartilages themselves being entirely passive in the matter. The extrinsic bands, again, must serve to protract the whole mass and thrust it more or less firmly against the object to be acted upon.

"I have examined Buccinum, Fisurella, Doris, Aplysia, Bullæa, Helix, Onchidium, Cypræa, Pteroceras, Sigaretus and Vermetus, and in all I have found a structure essentially similar to that here described ....

"This pulley-like structure of the tongue appears to me to be very characteristic of the portion of the molluscous type here considered [cephalous], and indeed to be peculiar to it" (Huxley, '53, p. 58, ff.).

Lacaze-Duthiers ('56) in his study on Dentalium describes the odontophoral apparatus fully and takes up the question of its mechanism. He concludes ('56, p. 258) that "the cartilage executes movements and communicates them secondarily to the dental apparatus."

In 1879, Geddes, at the suggestion of Huxley, took up the study of the odontophoral apparatus again, but arrived at just the opposite conclusion to that of the latter. He says in regard to Patella that "a slight sliding of the radula over the apex of the cartilages" may take place; but for Buccinum: "Little of that sliding movement over the apex of the cartilages which we saw in Patella can here take place, owing partly to the weakness and curvature in two planes of the cartilages, partly to the sharpness of their apex, eminently unfitting it for a pulley-block, partly to the slight fixed flexure of the radula, and its wants of pliability, and largely also to the attachment of the infraradular membrane to the sides of the mouth all round, which thus fixes the radula very steadily over

the cartilages. Some little yielding *may* take place; but it must be evident, from the above considerations, that the movements of the radula are similar to, and dependent upon, that licking action impressed upon the buccal cartilages in the way we have seen....

"Thus the explanation here put forward has something more in common with that of Cuvier....than with the later theory proposed by Professor Huxley....

"In the transparent bodies of some Heteropoda, Prof. Huxley describes a chain-saw movement; so, if the framework remains quite stationary, I can only suggest that the sliding of the radula over its support, which we saw as a secondary factor in the Limpet, though impossible in the Cuttlefish and highly improbable in the Whelk, may in these animals have acquired greater importance."

Tryon ('81) in his *Manual of Conchology* (continued by Pilsbry) gives nothing as to the mechanism of the odontophoral apparatus.

Wegmann ('84) describes the odontophoral apparatus in Haliotis and as regards the mechanism says ('84, p. 304): —

"No muscle is inserted upon the radula properly speaking; this organ is borne by the elastic membrane [radular membrane], with which it forms one body in its movements. The latter slides over the cartilages, drawn as it is by two pairs of protractor muscles and by numerous retractor bundles. Besides, the cartilages can be brought together or separated, increase and diminish the space between them. The elastic membrane is deeply influenced by these displacements and its own movements are thus complicated."

Boutan ('86) in his paper on Fissurella gives a brief description of the muscles of the odontophoral apparatus, but does not dwell upon the mechanism except to emphasize the importance of the blood sinuses in the proboscis. These during protrusion of the proboscis become filled with blood and produce turgidity of the organ, in fact, the protrusion is in part due to this turgid condition of the proboscis.

Bouvier ('87), while he gives a minute description of the nervous system of Buccinum and of many other Prosobranchs in his elaborate paper, does not describe the odontophoral apparatus at all fully.

Gibson ('87) describes the odontophoral apparatus of Patella but has nothing to say upon the subject of its mechanism.

Loisel ('92) describes the apparatus as found in Helix, and gives a rather confused account of its action.

Oswald, in 1893, published quite a detailed account of the "Rüsselapparat" of the Prosobranchs, dealing especially with the apparatus as found in *Buccinum undatum*. He describes at length the muscles that control the movement of the radula, as well as those concerned with the protrusion and withdrawal of the proboscis, and his descriptions are accompanied by a number of text-figures, schemata, and two plates. He also considers the mechanism of these parts. His observations for Buccinum closely parallel my own for Sycotypus, with some exceptions, and I find he suggested in a number of cases the very nomenclature I had adopted on my own account; for all my own observations had been made before the literature of the subject became accessible to me.

In regard to the rasping action of the radula, whether it is accomplished by the licking action of the cartilage or by active to and fro motion over the odontophoral cartilage, Oswald has the following to say ('93, pp. 146–147): "The motion of the radula is brought about by the contraction of its own muscles and at the same time by the movement of the cartilage. By the contraction of the approximators of the cartilage [rami] the anterior portions of the cartilages are brought nearer together, the radula is raised up, lying as it does over them, and, at the same time, pushed somewhat forward; the dorsal retractors relax, the ventral ones contract and the radula slides, as Huxley suggests, like a band over a pulley. The contraction of the approximators of the cartilage having ceased, the anterior ends of the cartilage by virtue of their elasticity separate, and at the same time the dorsal retractors pull the radula back. The sliding of the radula over the tongue cartilage in the manner of a band over a pulley is, it is true, very limited (sehr beschränkt), since the radula is fastened on both sides by its sheath to the mouth cavity; that, however, such a sliding motion does take place, has been made clear by my preparations, in which the radula was fixed in different stages of its excursion."

In the main Oswald's account of Buccinum accords with what I have observed for Sycotypus, but in Sycotypus, at least, the

motion of the radula over the cartilage as a band over a pulley is in no way "sehr beschränkt," for two to three centimeters of the length of the ribbon play back and forth over the head of the cartilage. One can easily convince oneself of the large excursions of the radula by placing one's finger tip in the mouth of an animal that has been placed in the alcohol-turpentine mixture, and that is consequently in no pleasant mood.

While Oswald states he made some observations on the living animal, he makes no reference to any detailed artificial stimulation of the muscles or nerves, and his conclusions as to the mechanism are, it seems, drawn to a considerable degree from the anatomy of the parts.

Plate ('93) gives a brief description of the odontophoral apparatus of *Oncidium verruculatum*, but does not dwell upon the mechanism, though since he speaks of retractors and protractors of the radula, he probably accepts a sliding action of that organ.

Amaudrut ('98) in a lengthy paper upon the anterior part of the alimentary canal in gastropods makes a comparative study of the odontophoral apparatus as found in this group of molluscs. He, however, does not describe that of Sycotypus. On page 145 of his article he begins a historical review of the question of the mechanism of "le bulbe," and the radula, which continues for some thirty pages. I refer anyone to them for a complete statement of the views put forth by various observers.

He himself absolutely rejects Huxley's view of the sliding action of the radula. He says ('98, pp. 137, ff., 147): "Every theory aiming at explaining the mechanism of the radula must take into account the facts which precede [certain anatomical relations, p. 84] and the remarks which follow:

"The radula being flexible and having to function as a rasp must when in use always have a certain degree of tension. Now the rasp being united to the elastic membrane [radular membrane] its movements become subordinated to those of this membrane, and since the muscles and cartilages are connected only with the membrane and not with the rasp it is through the tension of the membrane that the tension of the rasp is secured. But this tension can be produced upon the whole membrane only by the simultaneous contraction of the muscles that act upon it, for every movement of traction exerted upon one point only would

entail a sliding of the membrane — a thing which anatomical examination has shown us as being impossible (Fig. 45, Pl. V) [the figure is for *Helix pomatia*, but his assertion is a general one, see p. 147, and refers to Prosobranchs too], and which direct observation has never established [?]. Further, a traction produced upon one point only of the membrane would occasion in it not only a sliding motion but also the production of folds in it, and then, whether the flexible radula should follow the contours of the folded surface or whether it should pass beyond, in either case it would be in an unfit state for playing its rôle of rasp."

It is clear therefore that Amaudrut regards as *tensors* what other observers and I have considered as protractors and retractors of the radula. So far as Sycotypus is concerned he is in error, for by direct observation one can easily convince oneself of the sliding motion of the radula in this large gastropod.

His explanation is as follows: "The important differences in the general mechanism which exist between the *Pulmonata* and the *Rachiglossa*, are that, with the latter when the flexors [protractors] of the cartilages contract, the summit of the tongue is not only drawn forward, but the lateral teeth separate, and when the tensors [of the radular membrane] contract in their turn, the teeth execute the reverse movement, seize the prey and carry it to the entrance of the œsophagus."

Direct observation of the action of the radula seems to have been confined, on Amaudrut's part, exclusively to Helix. His explanation of the mechanism for this form is doubtless correct, but he has certainly gone too far when he makes the general assertion that a sliding motion of the radula is *impossible*. On the contrary it has been observed by Huxley and a number of other observers, as we have seen above.

Simroth (:01) follows Amaudrut in his description of the mechanism of the odontophoral apparatus among the Prosobranchs. Under the heading, "Der Fressact" he says (:01, pp. 490–491): "The act of eating is accomplished in general in this way: — The bulb executes regular piston-strokes from behind forward and the tip of the tongue simultaneous twisting movements downwards and backwards extending to the entrance of the esophagus. In the forward position the teeth of the tip of the tongue grasp the mouthful from beneath, then it is drawn in, cut off by pressure

against the immovable jaw where such an organ occurs, and, without lingering at all in the bulb, pushed into the esophagus. The radula suffers thereby no shifting of any sort (keinerlei Verschiebung) upon its support."

Pelseneer (:06, p. 7) in his volume on the Mollusca in Lankester's *Treatise*, speaking of the odontophoral apparatus, has the following remarks: "Applied to these cartilaginous pieces the radula, by the action of special muscles, executes backward and forward rasping movements."

Again (:06, p. 89): "The radular ribbon is supported by a system of paired cartilaginous pieces furnished with protractor and retractor muscles the action of which causes the radula to move to and fro and work like a rasp on the prey seized by the animal."

From this review it is evident that the mechanism of the radula is conceived of in two very different ways by *most* of the observers that have up to the present worked upon it: —

(1) The radula remains at rest relatively to its support (the cartilage) and its rasping action is due to movements of its support.

(2) The radula moves relatively to its support, plays back and forth over its support like a band over a pulley, and its rasping action is due to its own proper motion.

I hope to show conclusively in what follows that the action of the radula in Sycotypus is of the band-over-pulley type. I do not desire to generalize from observations upon one form, and that an isolated one, Sycotypus being found only "along the Atlantic coast of North America from the south shore of Cape Cod, to the Gulf of Mexico" (Grabau, this journal, vol. 37, pp. 515–539). However, from a study of the figures given by Geddes and others for Buccinum, I cannot help thinking that a renewed study of this animal under experimental conditions will reveal the fact that the play of the radular ribbon is not altogether "very limited," as Oswald concedes.

Description of Odontophoral Apparatus

Since this apparatus is found in the proboscis of the animal, it will be well to commence with this organ. As I intend to give the nervous supply of the muscles described, it is advisable to take up the nervous ganglia after the proboscis. Following the brief description of the ganglia, will be taken up in order: the esophagus and buccal mass; the buccal cartilage, its retractor and protractor muscles; the radula, its retractors and protractors; and finally the musculature of the proboscis, and the mechanism of its protraction and retraction.

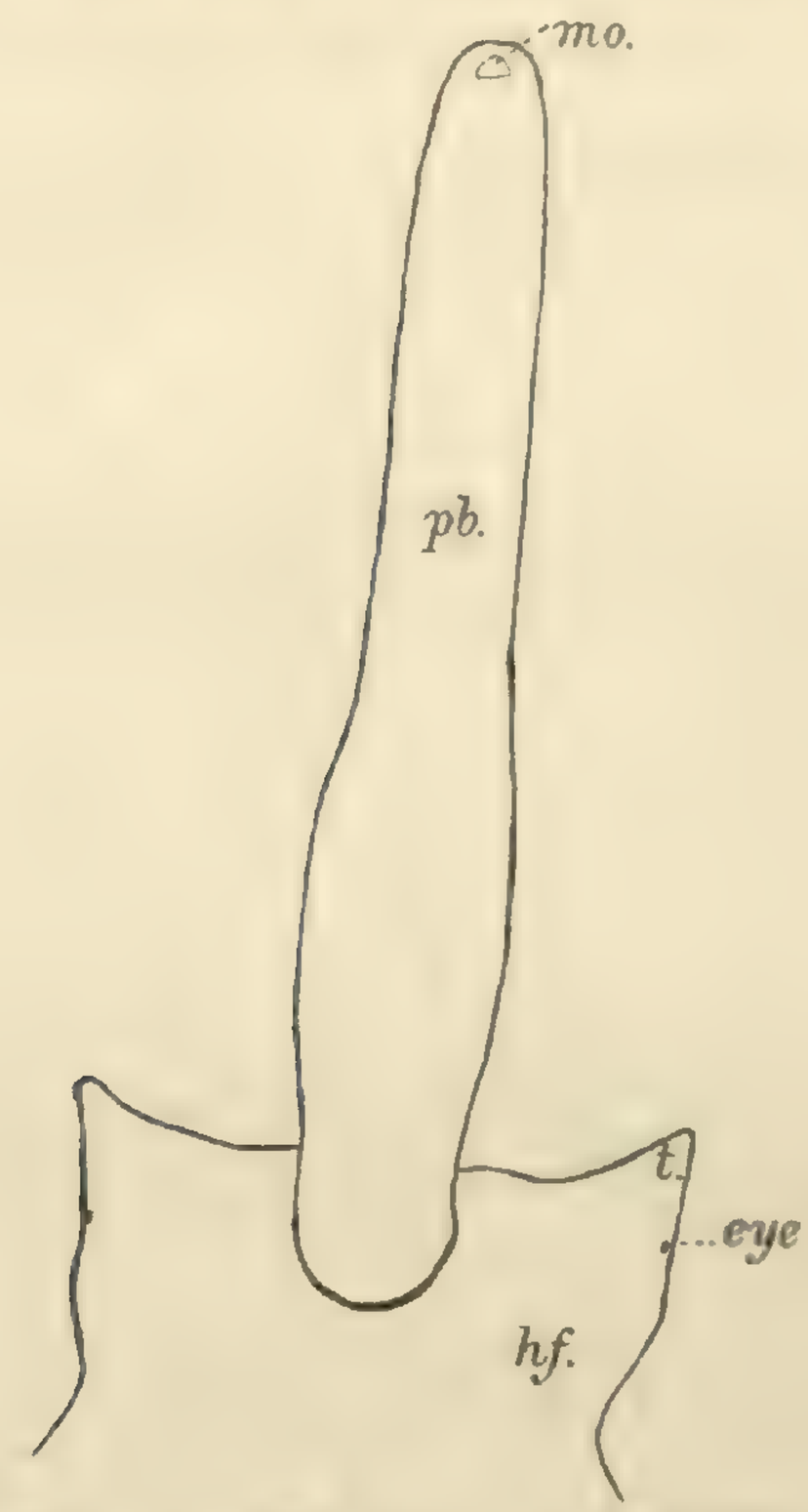

Fig. 1. — *Sycotypus canaliculatus*. Ventral view of the fully extended proboscis. *hf.*, head fold; *mo.*, mouth; *pb.*, proboscis; *t.*, tentacle.

Proboscis.— Many of the Prosobranchs possess a long proboscis, sometimes longer than the rest of the animal. In Sycotypus this organ is well developed, the fully extended proboscis being in a fair-sized specimen three or four inches long. The proboscis when protruded emerges from the head fold (Fig. 1, *hf.*) which surrounds its base like a collar, there being a deep groove between the two, formed by the invagination of the integument. The anterior half of the organ is almost circular in section, and hard to the touch, while the posterior half is more flattened and flabby. At the end of the proboscis is located the triangular mouth — bounded by thick and hard lips — the base of the triangle being ventral. When retracted the proboscis is completely hidden from view; it lies entirely within the head fold, which is drawn together so as to hide the opening through which the proboscis is put forth.

The proboscis has a tough muscular wall, invested by integument which is closely adherent to the underlying muscular layers. At the base of the proboscis is a cup of white muscular fibers

through which the esophagus passes and into which some of the retractors of the proboscis (to be dealt with later) are inserted (Fig. 2, *rpb.*).

The proboscis is a hollow tube containing within it the esophagus and the large cylindrical mass, called the *buccal mass*.

Nervous Ganglia.—The ganglia lie below the base of the proboscis (in its protruded state) in the deep part of the head fold

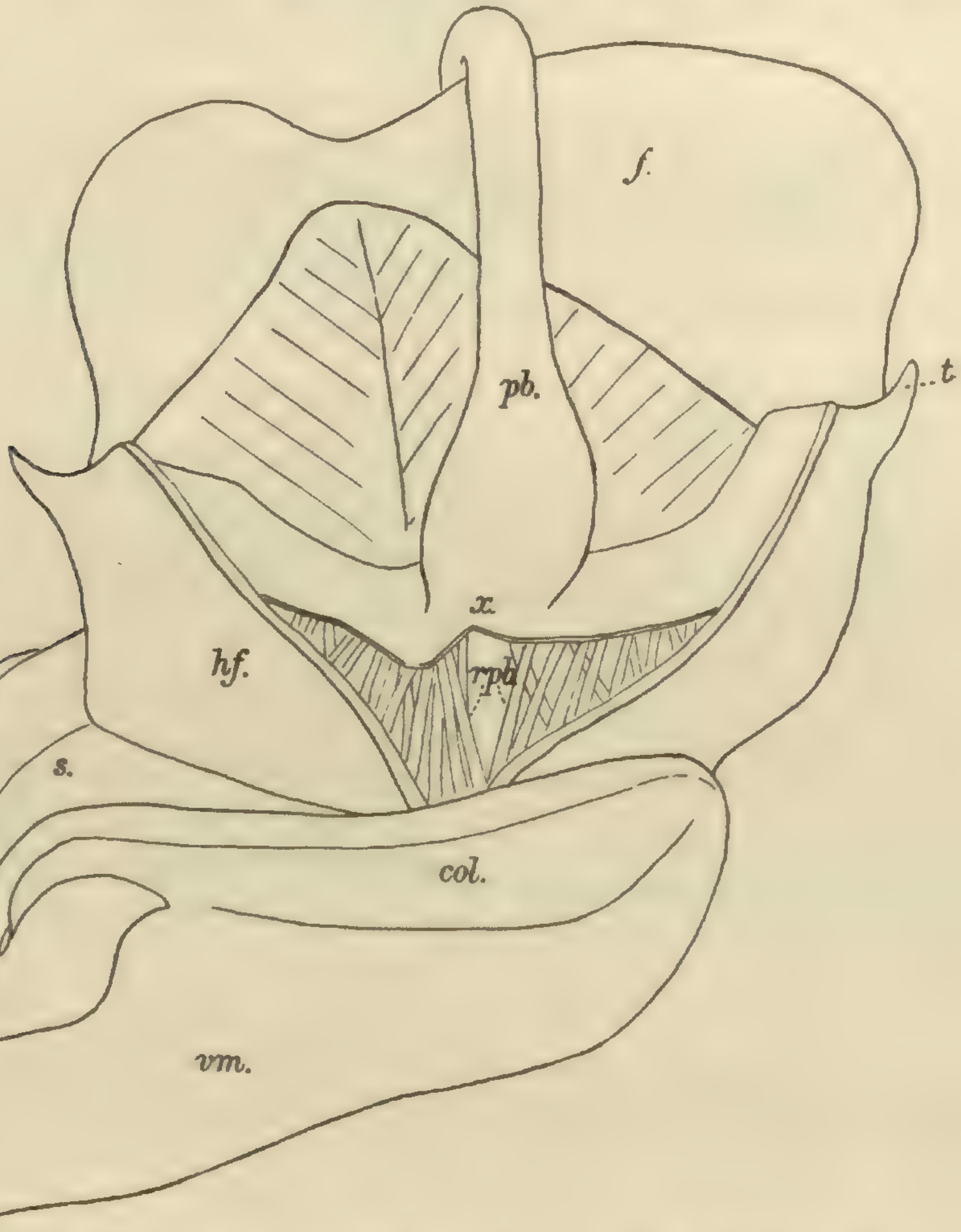

FIG. 2.—*Sycotypus canaliculatus.* Dissection from the dorsal aspect. Head fold laid open dorsally and ventrally; foot split open; proboscis hangs down over the foot. *col.*, collar; *f.*, foot, split open; *hf.*, head fold; *pb.*, proboscis; *rpb.*, retractors of proboscis; *s.*, siphon; *t.*, tentacle; *vm.*, visceral mass; *x*, position of ring muscle.

and surround the esophagus (Fig. 3, *ng.*). The ganglia comprise: the buccal, two small spherical ganglia closely adherent to the ventral surface of the esophagus and united by a commissure; the two cerebral ganglia; the pleural ganglia; the crossed visceral pair; and the large pedal ganglia. Their relations are presented in the accompanying diagrammatic figure (Fig. 4).

Nerves arise from these ganglia and are distributed to various parts of the body; but those that will be especially dealt with here are the ones that arise from the buccal and the cerebral ganglia.

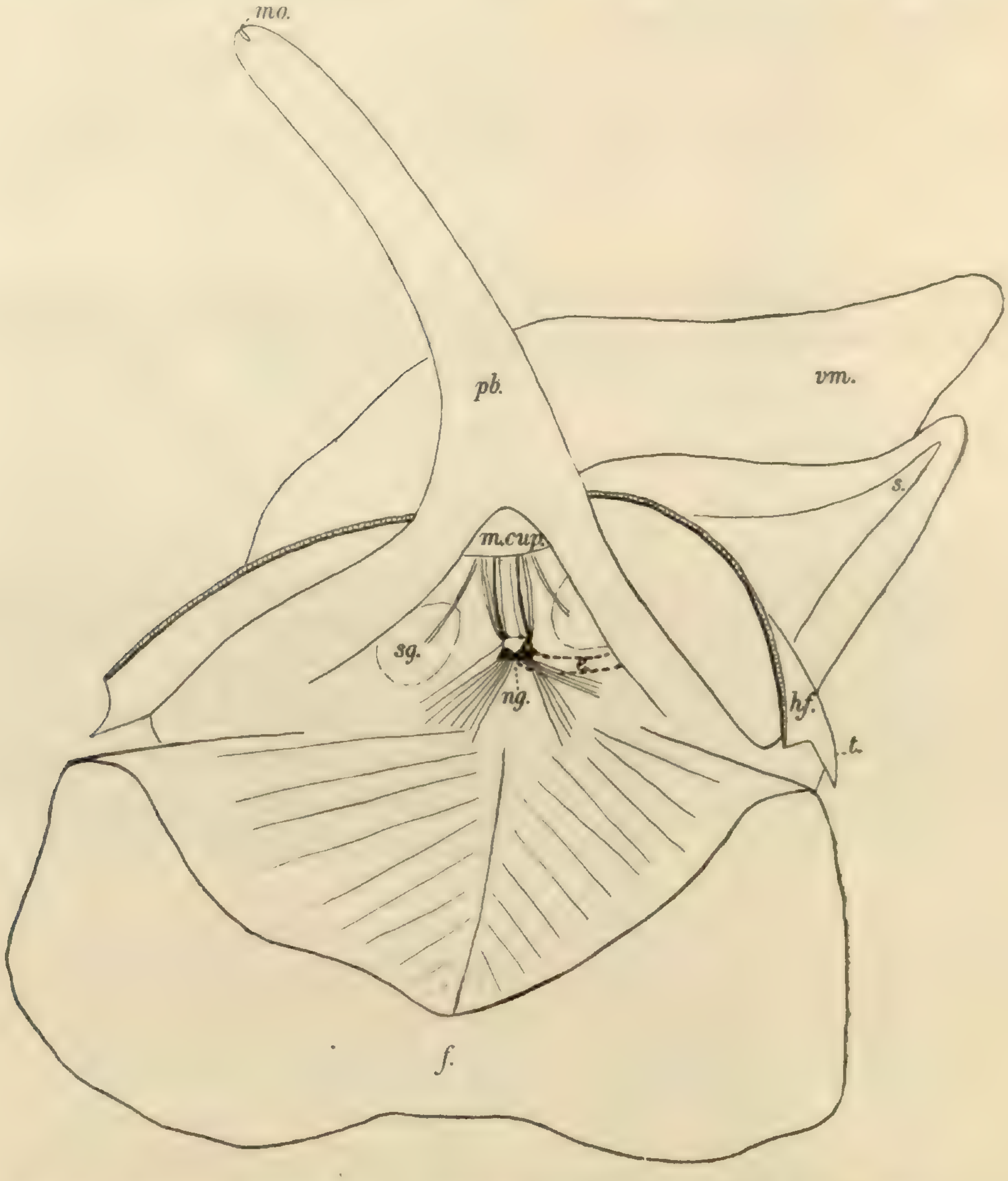

FIG. 3.— *Sycotypus canaliculatus*. Dissection from the ventral side (semidiagrammatic) showing relation of the various parts of entire animal after removal from shell: head fold, as also proboscis, laid open; foot split partially through so as to display ganglia *in situ*. *e.*, esophagus; *f.*, foot, split through; *hf.*, head fold; *mo.*, mouth; *m. cup*, muscular cup; *ng.*, ganglia; *pb.*, proboscis; *s.*, siphon; *sg.*, salivary gland; *t.*, tentacle; *vm.*, visceral mass.

From each buccal ganglion arise two nerves, one stout (inner), the other very slender (outer). From the cerebral ganglion arise

five or six anteriorly directed nerves, and one directed laterally which passes out across the salivary gland into the tentacle to supply that organ and the eye. The distribution of the forwardly directed nerves we shall see later. As they pass forward they anastomose more or less.

The buccal and cerebral ganglia of each side are connected by a

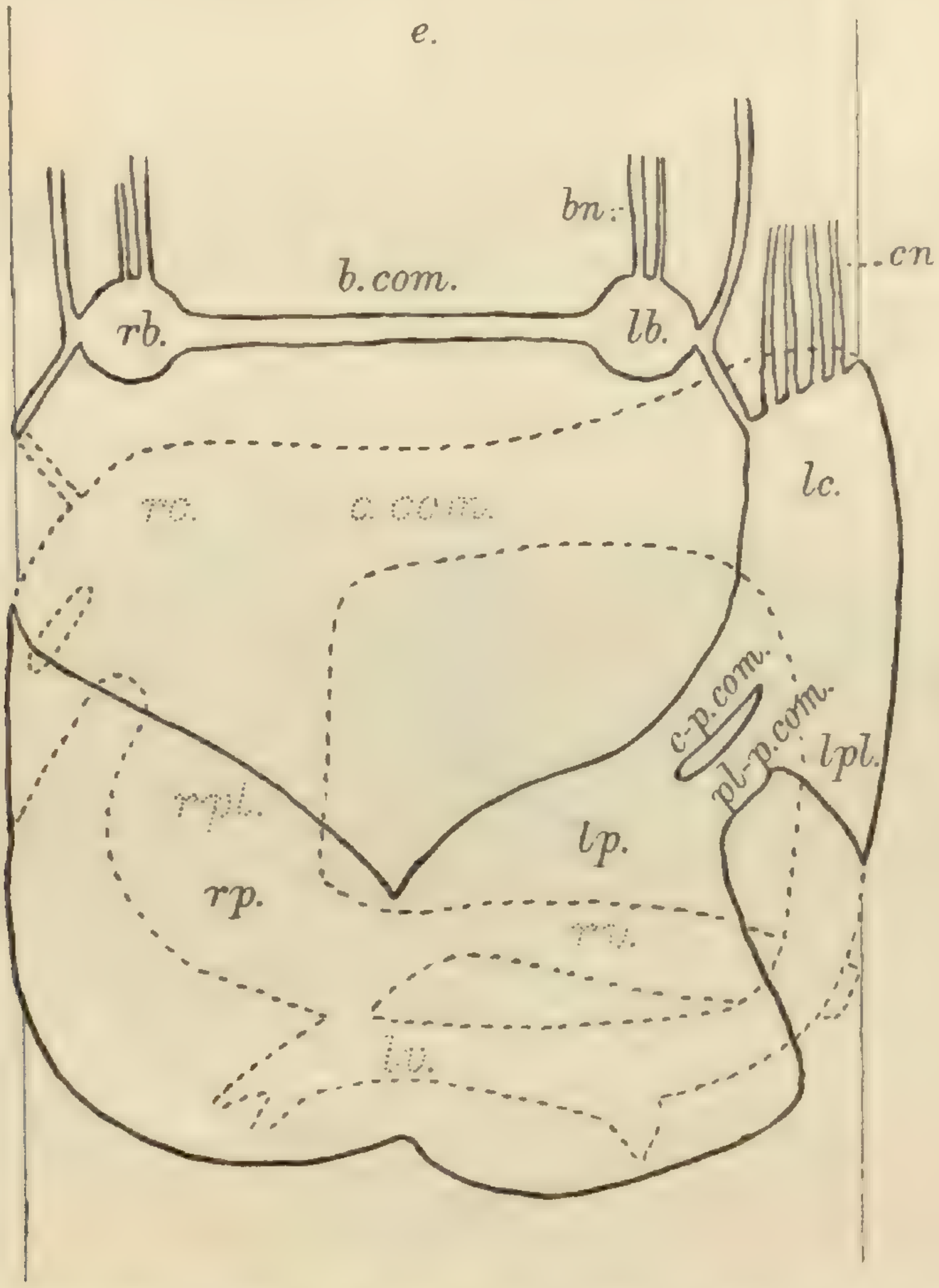

FIG. 4.— *Sycotypus canaliculatus*. Ventral view of the ganglia that surround the esophagus (diagrammatic, from several drawings of dissections); the ventral side of the ring is in full line, the dorsal in dotted line, and the outline of the esophagus is indicated by the light parallel lines. *b. com.*, buccal commissure; *bn.*, buccal nerves; *c. com.*, cerebral commissure; *cn.*, cerebral nerves; *c-p. com.*, cerebro-pedal commissure; *lc.*, left cerebral ganglion; *lpl.*, left pleural ganglion; *lp.*, left pedal ganglion; *lv.*, left visceral ganglion; *pl-p. com.*, pleuro-pedal commissure; *rb.*, right buccal ganglion; *rc.*, right cerebral ganglion; *rp.*, right pedal ganglion; *rpl.*, right pleural ganglion; *rv.*, right visceral ganglion.

very short commissure passing between the most median nerve coming off from the cerebral and the buccal ganglia (Fig. 4).

Esophagus and Buccal Mass

As stated above, the esophagus and the buccal mass lie within the proboscis. Whereas the esophagus is closely adherent to the dorsal wall of the proboscis (numerous muscle fibers passing between the two), the buccal mass lies free within the proboscis, except at the anterior and posterior ends where muscles are inserted into the wall of the proboscis (Fig. 5). At the anterior end the buccal mass is also united with the esophagus by a thin membrane (Fig. 5, *m.*). Consequently if the proboscis be split open along the ventral surface, the entire buccal mass may be removed without in any way injuring the esophagus, except at its commencement where it is united to the buccal mass (Fig. 6).

We thus have three tubes, one of which (the proboscis) contains the two others, the esophagus being dorsal, and the buccal mass ventral. In cross section they would appear as shown in Fig. 7.

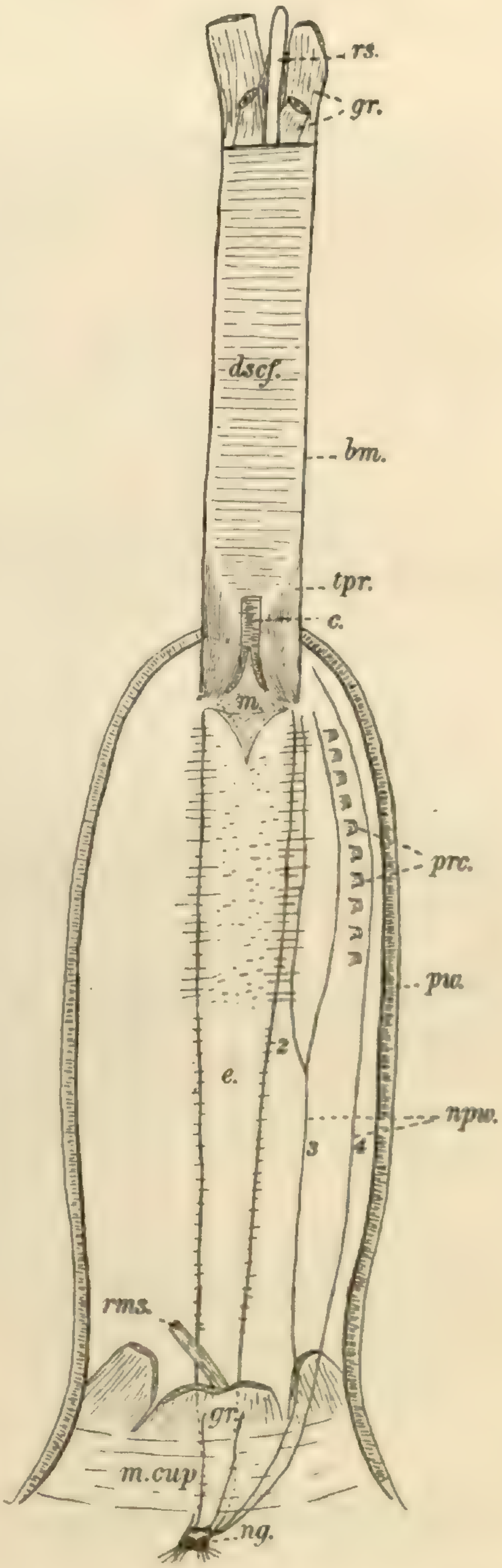

Fig. 5.— ***Sycotypus canaliculatus.*** **Ventral view; the proboscis has been laid open along the mid-ventral line, and the buccal mass has been resected and turned back.** *bm.*, buccal mass; *c.*, cartilage, edges of; *dscf.*, dorsal sheet of cross fibers; *e.*, esophagus; *gr.*, great retractor; *m.*, membrane at junction of buccal mass and esophagus; *m. cup*, muscular cup; *ng.*, ganglia; *npw.*, *2*, *3*, *4*, nerves to proboscis wall; *prc.*, protractors of cartilage, cut across; *pw.*, **proboscis wall;** ***rms.*, radular muscle;** ***rs.*, radular sac;** ***tpr.*, triangular protractor.**

ODONTOPHORAL (BUCCAL) CARTILAGE

The radula or dentated ribbon is essentially a thin flexible file which is worked back and forth over the odontophoral cartilage. By the protraction or retraction of this cartilage over which the radula runs like a strap over a pulley, the lingual file (or better, rasp) is either brought forward into the mouth to a position where, aided by the hard lips, rasping can be effected, or (on retraction) it can be carried back out of the way.

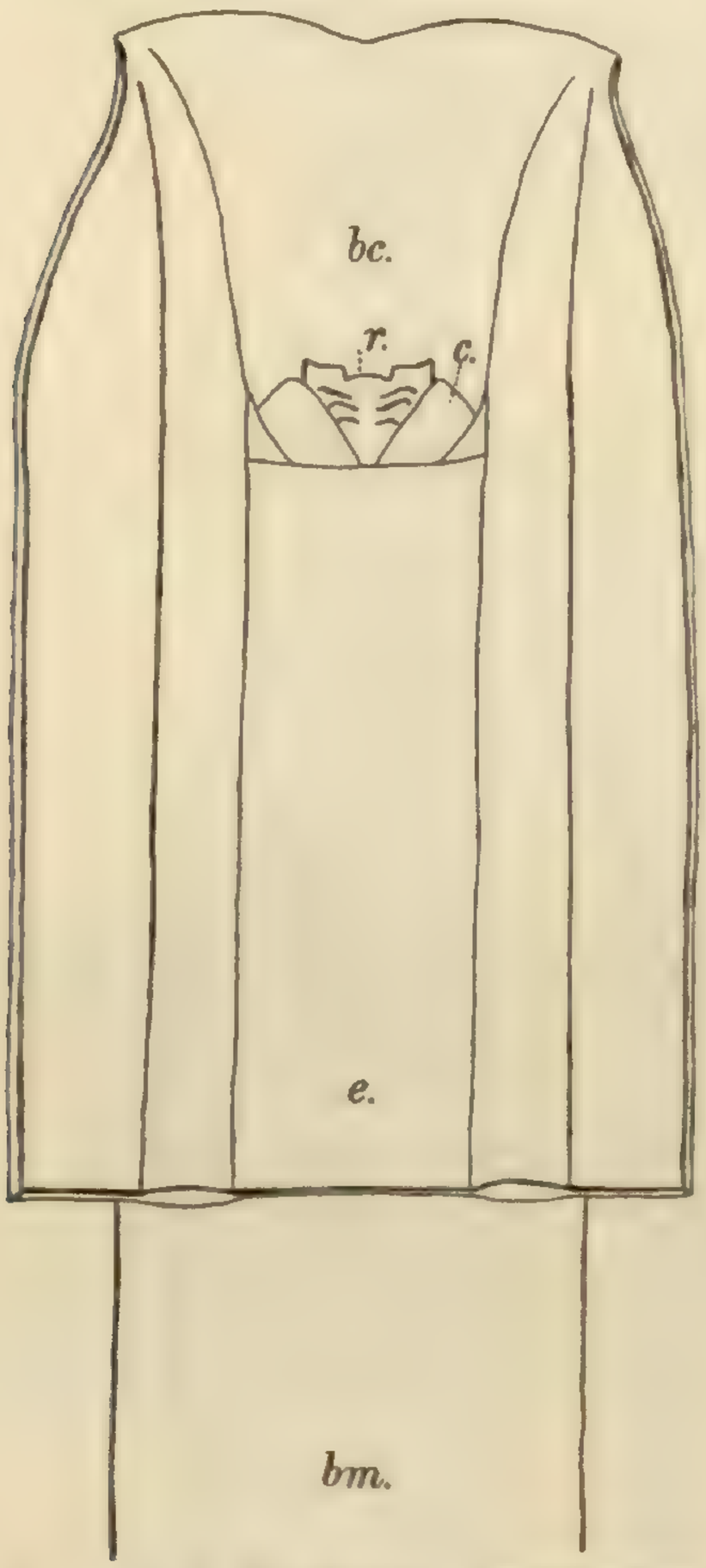

FIG. 6. — *Sycotypus canaliculatus.* Dorsal view; buccal cavity and esophagus have been opened along mid-dorsal line, and the esophagus in part cut away, thus exposing the buccal mass beneath; the proboscis wall has been entirely dissected away. *bc.*, buccal cavity; *bm.*, buccal mass; *c.*, cartilage covered by radular membrane; *e.*, esophagus; *r.*, radula.

The cartilage has two long *rami* that unite anteriorly to form a *head* (Fig. 8), the entire length being from five to six centimeters in a fair-sized specimen. The cartilage has somewhat the form of a toboggan that has been split up along the running part to near the upturned front; the front has been turned in laterally, so that its rim is no longer straight, as in a toboggan, but horseshoe-shaped. The rami are deeply grooved dorsally and the grooves are continued forward on the dorsal, or rather posterior surface, of the upturned head. It is in these grooves that the muscles retracting the ribbon run. The ribbon itself passes over the rim of the head of the cartilage as

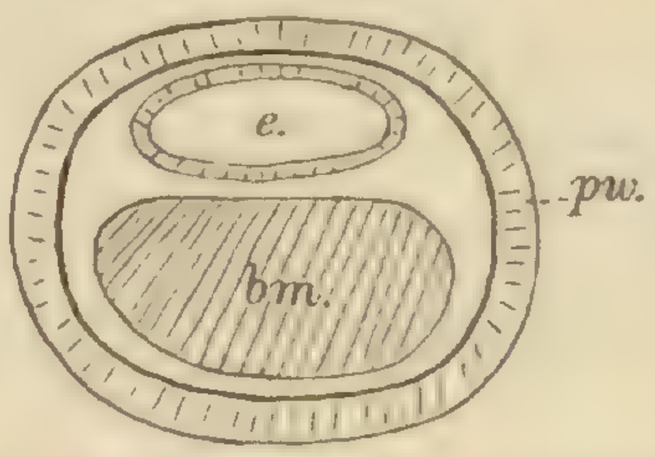

FIG. 7.— *Sycotypus canaliculatus.* Diagram to show relation of esophagus and buccal mass. *bm.*, buccal mass; *e.*, esophagus; *pw.*, proboscis wall.

over a pulley (Fig. 8, *rim*). Since the rim is not straight but horse-shoe-shaped, the ribbon is folded together as it passes back over the cartilage, and unfolded as it passes forward; otherwise the animal would rasp its own tissues. As it is, the lateral teeth (Fig. 13, *lt.*) are turned in against each other, so that as the lingual ribbon passes back from the head of the cartilage they are thrown out of action. This is a very important point in the mechanism, and one which has not been insisted upon. The shape of the head of the cartilage is perfectly adapted for this folding and unfolding of the ribbon as it plays backward and forward.

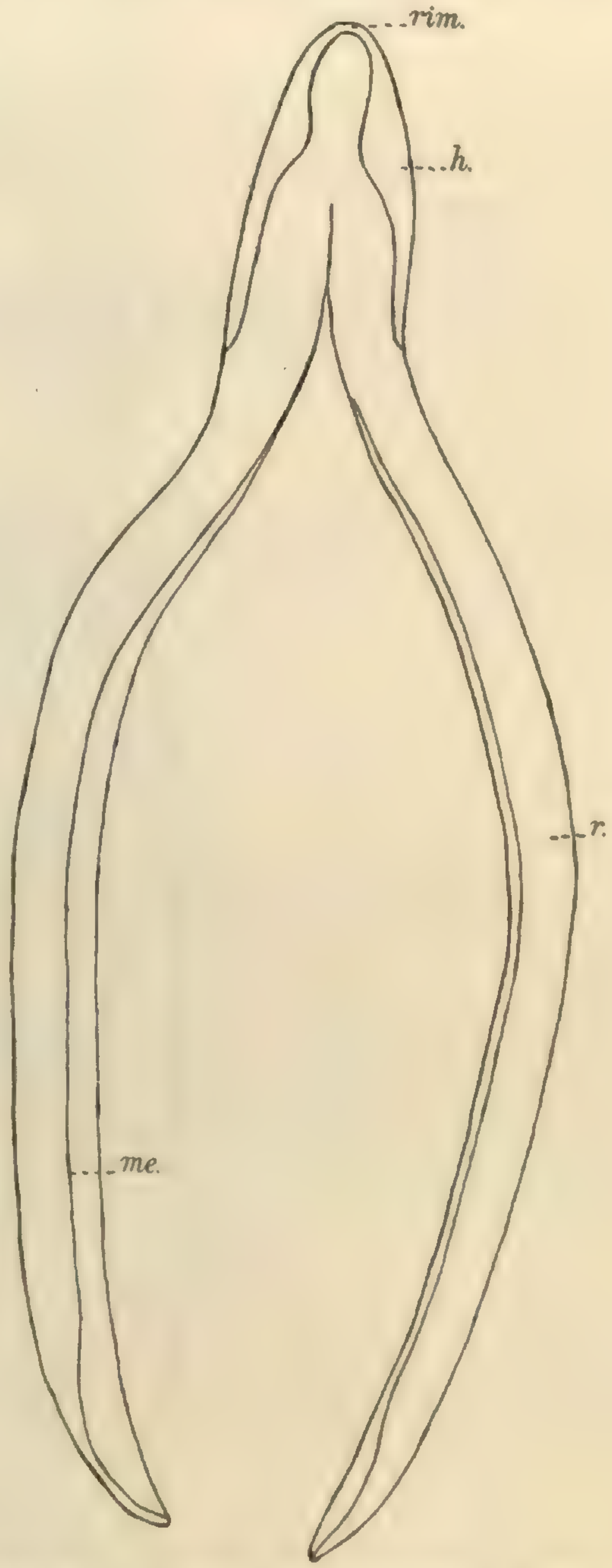

FIG. 8.— *Sycotypus canaliculatus*. Dorsal view of odontophoral cartilage, stripped of its muscles; the grooved surfaces of the rami face somewhat outward. *h.*, head; *me.*, median edge; *r.*, ramus; *rim*, the pulley-like portion of the head.

The grooved surfaces of the rami and head furnish a very smooth running surface for the retractor muscles and their tendons.

A ramus in cross section is moon-shaped. Muscles find a place of attachment along the lateral edge, but the median edge is thin and free of muscle insertions. A line of muscular attachment runs along the convex side of each ramus on the median aspect. This line marks where a sheet of cross muscle fibers passes from one ramus to the other binding them together. To the posterior end of the ramus are also attached muscles.

In Fig. 8, the rami of the cartilage are spread apart since the muscles binding them together have been cut through. In the

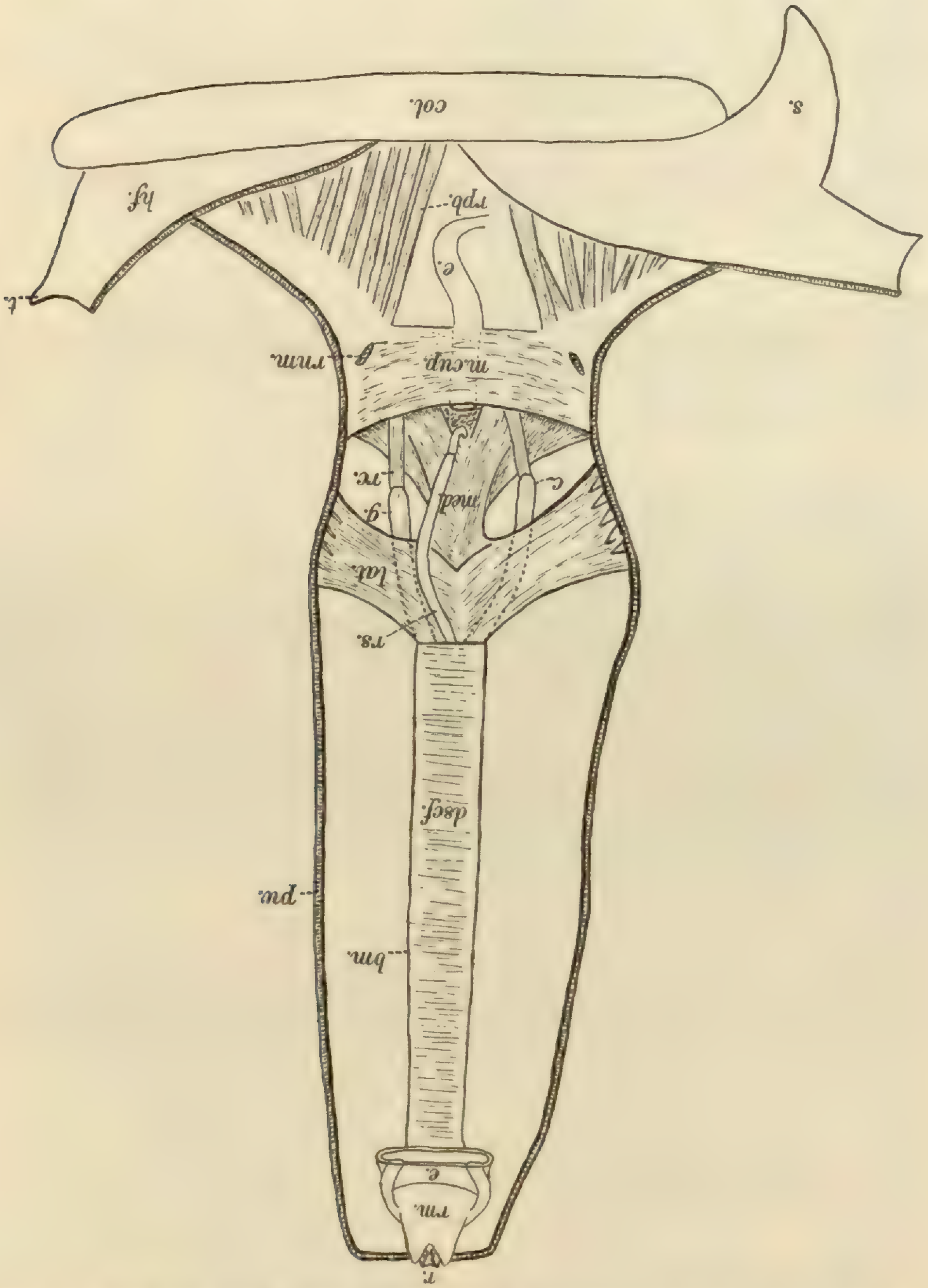

FIG. 9.— *Sycotypus canaliculatus.* Dorsal view; the proboscis has been laid open in its entire length; the esophagus has been resected and removed; the head-fold has been split open; the protractors of the cartilage are omitted. *bm.*, buccal mass; *c.*, cartilage, ramus of; *col.*, collar; *dscf.*, dorsal sheet of cross fibers; *e.*, esophagus; *g.*, groove root of great retractor: *hf.*, head fold; *lat.*, lateral root of great retractor; *med.*, median root of great retractor; *m. cup*, muscular cup; *pw.*, proboscis wall; *r.*, radula; *rm.*, radular membrane; *rnm.*, ring muscle of cup; *rpb.*, retractors of proboscis; *rs.*, radular sac; *s.*, siphon; *t.*, tentacle.

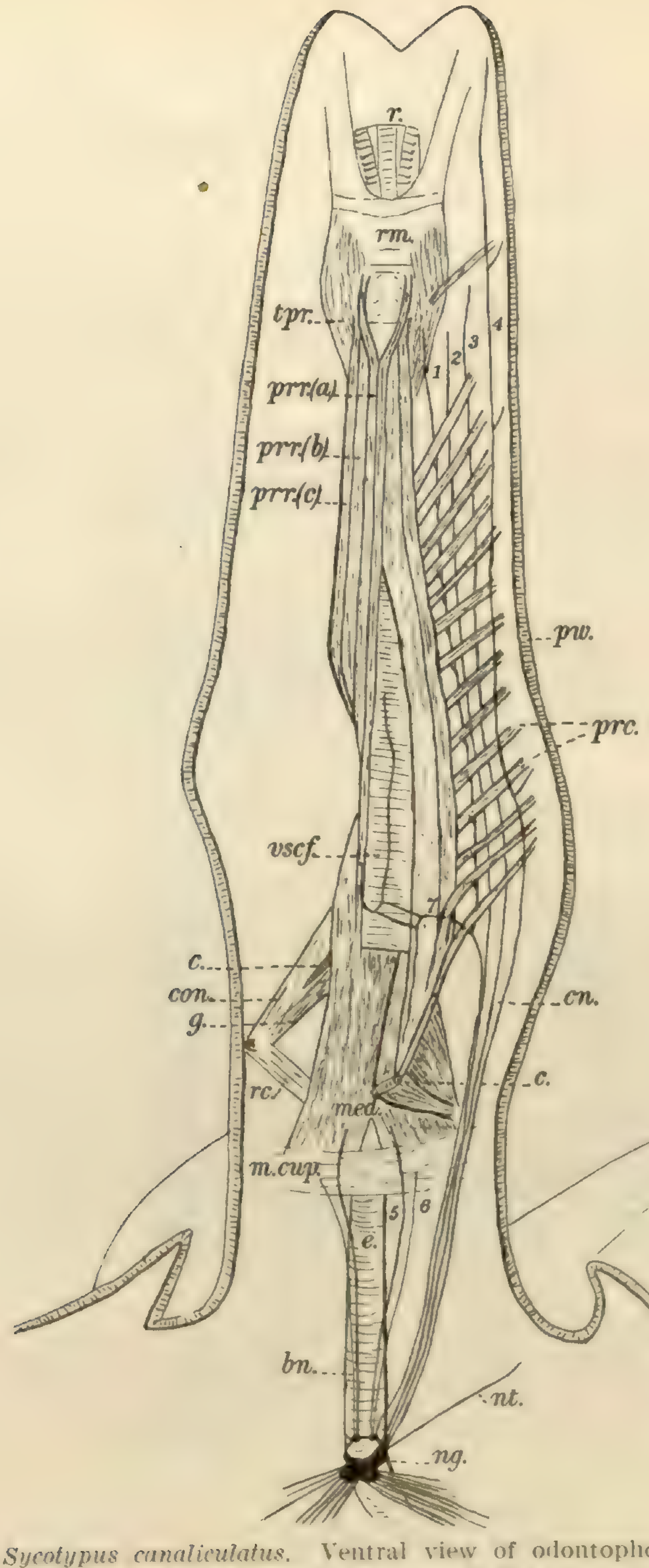

FIG. 10.— *Sycotypus canaliculatus*. Ventral view of odontophoral muscles, the proboscis and head fold having been opened; the odontophoral cartilage has been twisted somewhat to the right (of the animal) so as to bring its protractors into prominence (those on the right side are omitted), and also to expose the nerves that are to be seen in the left half. *bn.*, nerves from buccal ganglion; *c.*, cartilage; *cn.*, nerves from cerebral ganglion; *con.*, convex root of great retractor; *e.*, esophagus; *g.*, groove root of great retractor; *m. cup*, muscular cup; *med.*, median root of great retractor, the lateral root is omitted; *ng.*, ganglia; *nt.*, nerve to tentacle; *prc.*, protractors of cartilage; *prr.* (*a*, *b*, *c*), protractors of radula; *r.*, radula; *rc.*, retractor of cartilage; *rm.*, radular membrane; *t.*, tentacle; *tpr.*, triangular protractor of cartilage; *vscf.*, ventral sheet of cross fibers; *1*, nerve supplying protractors of cartilage; *2*, *3*, and *4*, nerves supplying proboscis wall; *4* has been dissected out, and lies upon the cartilage protractors; *5*, stout nerve from buccal ganglion which enters great retractor; *6*, slender nerve from buccal ganglion; *7*, nerve that branches off from *1* and supplies protractors of radula and ventral sheet of cross fibers.

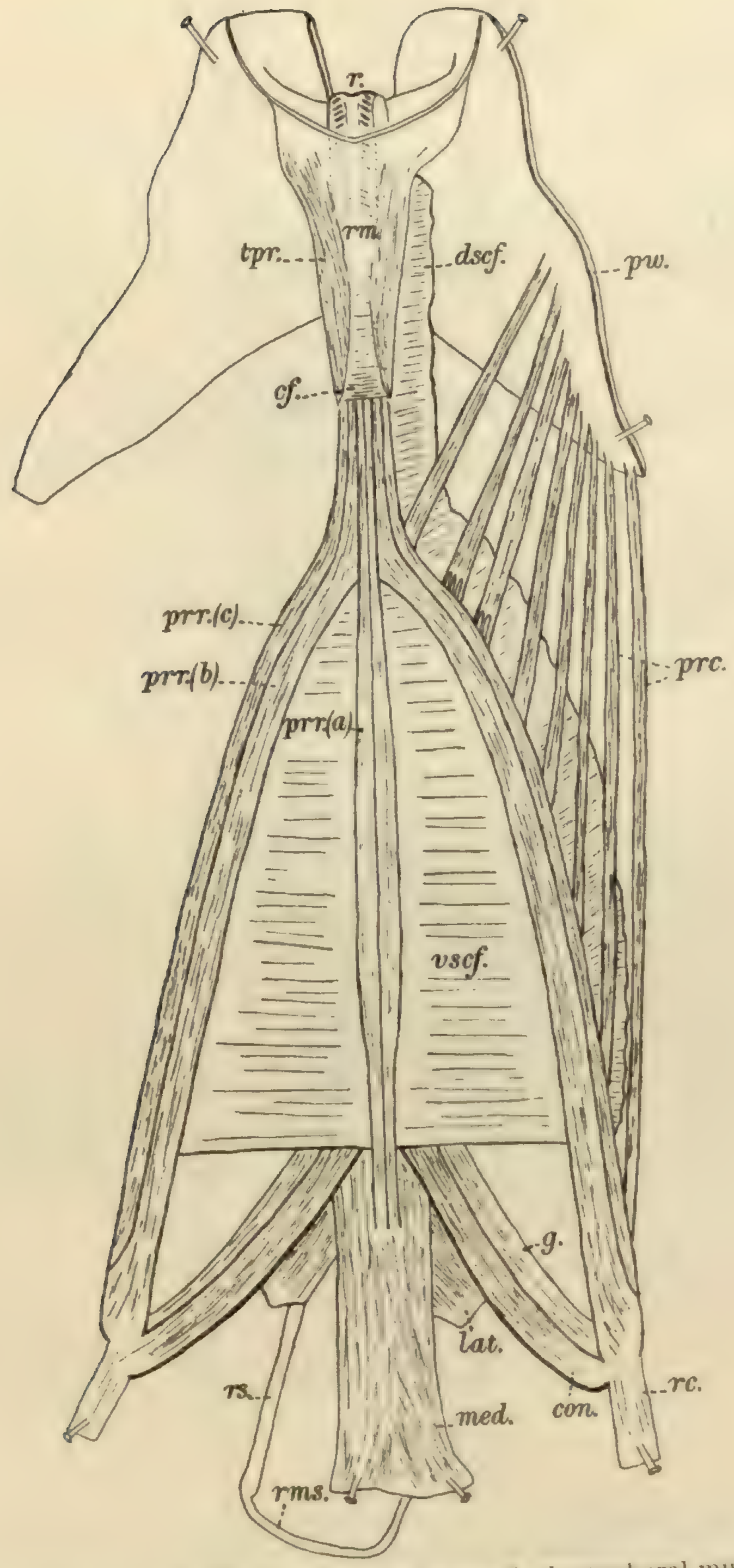

FIG. 11.— *Sycotypus canaliculatus*. Ventral view of odontophoral muscles, some of which have been cut through; the entire wall of the proboscis has been removed except that portion into which the protractors of the cartilage are inserted; the whole buccal mass is pinned out so as to display the several muscles, the dorsal sheet of cross fibers having been cut through; all of the muscles are drawn on the right of the figure only. *cf.*, cross fibers uniting triangular protractors, cut through in Fig. 10; *con.*, convex root of great retractor; *dscf.*, dorsal sheet of cross fibers, cut through; *g.*, groove root of great retractor; *lat.*, lateral root of great retractors; *med.*, median root of great retractor; *prc.*, protractors of cartilage; *prr.* (*a*, *b*, *c*), protractors of radula; *pw.*, proboscis wall; *r.*, radula; *rc.*, retractor of cartilage; *rm.*, radular membrane; *rms.*, radular muscle; *rs.*, radular sac; *tpr.*, triangular protractor of cartilage; *vscf.*, ventral sheet of cross fibers.

natural state the rami are closely approximated for most of their course, and form the doubly grooved roadway for the retractors of the lingual ribbon.

Retractors and Protractors of the Odontophoral Cartilage — Their Nerve Supply

Retractors.— These are two flat muscles which arise from the posterior extremities of the rami of the cartilage, and pass back one on each side to mingle with the fibers of the muscle cup at the base of the proboscis (Fig. 9, *rc.*). They serve to pull the cartilage — the whole buccal mass in fact — backward.

Their *nervous supply* comes through the stout nerve from the buccal ganglion (Fig. 10, *5*).

Protractors.— The protractors of the cartilage are conspicuous

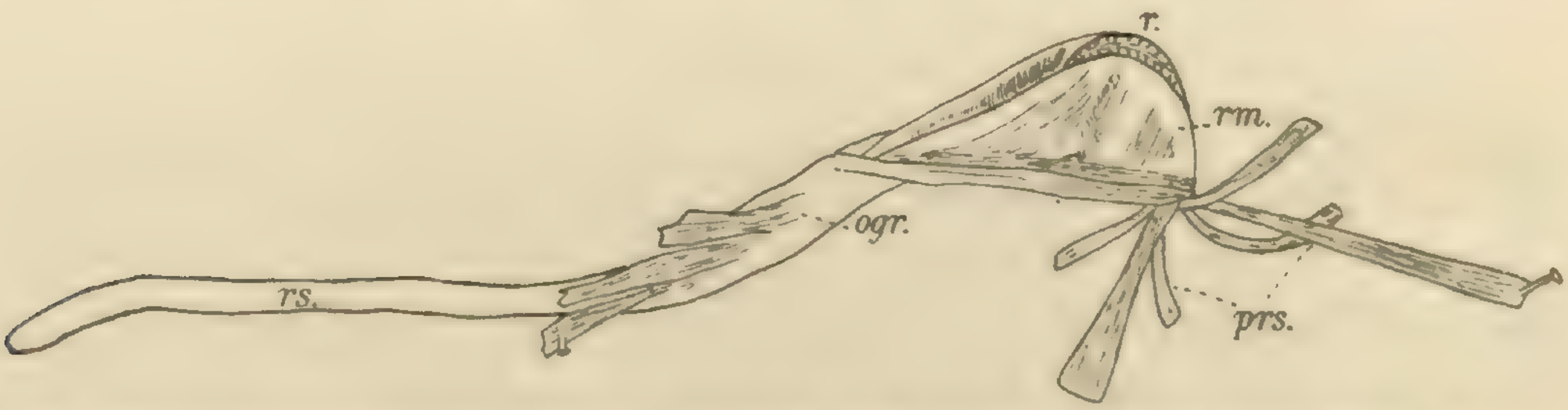

Fig. 12.— *Sycotypus canaliculatus.* Radular sac, radular membrane, radula, and its protractors removed from the proboscis and pinned out. *ogr.*, place of origin of great retractor; *prs.*, protractors of radula; *r.*, radula; *rm.*, radular membrane; *rs.*, radular sac.

narrow muscle bands (ten to twelve or more in number) that arise from the lateral edges of the rami and pass forward to be inserted into the ventral wall of the proboscis along two parallel lines, (Figs. 10, 11, *prc.*). Besides these bands there is also a pair of protractors that lie on either side of the buccal mass at its anterior end (Figs. 10, 11, *tpr.*). Each is more or less triangular in shape, the apex and dorsal edge lying along, and inserted into the lateral edge of the cartilage ramus, and the base being inserted into the radular membrane, and into the muscular wall of the buccal cavity laterally and dorsally. The ventral edges of the two *triangular protractors* are united by cross fibers, which serve to keep the underlying muscles (protractors of the radula) in place (Fig. 11, *cf.*).

All these muscles pull the cartilage forward in the proboscis, and it is by means of them that the dentate ribbon, which passes over the rim of the head of the cartilage, is brought forward into position for rasping.

Their *nervous supply* comes through one of the nerves of the cerebral ganglion. The nerve on each side runs along beneath the protractors near their origin, sending branches to each, and ends forward in the triangular protractor (Fig. 10, *1*).

RADULA (LINGUAL OR DENTATE RIBBON)

The radula is a dentate ribbon which is adherent to the membrane — *radular membrane* (*subradular membrane*) — that lines

FIG. 13.— *Sycotypus canaliculatus*. Radular teeth. *mt.*, median tooth; *lt.*, lateral tooth.

the buccal cavity (Fig. 12, *rm.*). The membrane lies loose over the head of the odontophoral cartilage, and passes back into what is called the *radular sac* (Fig. 12, *rs.*), which contains the immature part of the ribbon, and anteriorly it is produced into a pouch which lies on the ventral side of the anterior part of the buccal mass beneath the cross fibers that connect the ventral edges of the triangular protractors already mentioned (Figs. 10, 11, *rm.*). Laterally the membrane passes into the general lining of the buccal cavity. The membrane on the floor of the buccal cavity is loose enough to admit of the protraction of the head of the odontophoral cartilage a centimeter beyond the mouth, *i. e.*, in forced protraction,

not in the living animal. The looseness of the membrane thus allows of the forward and backward play of the ribbon in rasping. The muscles that are responsible for the rasping movements of the ribbon *are not attached to the ribbon* directly, but to *the membrane* to which the ribbon is adherent (the radular membrane). By treatment with alcohol the ribbon is readily separated from its membrane. That part of the ribbon which is mature and in use is from three to four cm. long, whereas the immature part which is folded up within the radular sac, and which cannot be drawn out over the rim of the cartilage head is some five cm. long.

It is to the radular sac that the large retractors of the ribbon are attached, the protractors being attached to the ventral pouch of the radular membrane (Fig. 12, *prs.*, *ogr.*).

Retractors and Protractors of Radula; Certain Accessory Muscles — Their Nerve Supply

Retractors (together with Certain Accessory Muscles).— The retractors of the lingual ribbon are, as above stated, inserted by tendons into the radular sac. At the region of their insertion they are fused so as to form practically one muscle, but posteriorly four separate roots can be distinguished (Figs. 9, 11, 14): —

(1) A large *median root* (Figs. 9, 11, *med.*), separable into lateral halves, passes back to be inserted on either side into the lateral and ventral wall of the proboscis and into the muscular cup at the base of the proboscis.

(2) Two large *lateral roots* (Figs. 9, 11, 14, *lat.*), which are continuous anteriorly with the median, pass outward on either side and are inserted by a half dozen bundles into the lateral wall of the proboscis somewhat anteriorly to the insertion of the median root. In passing out to the wall of the proboscis, this muscle crosses over the posterior portion of the ramus of the odontophoral cartilage, and hence serves to hold it in place (Fig. 9).

(3) A slender root passes back in the posterior part of the groove on the dorsal surface of each ramus of the cartilage — *groove root* (Figs. 9, 11, 14, *g.*). These roots are inserted at the tips of the rami, and are continuous anteriorly with the lateral roots.

(4) Another slender root on each side passes back beneath (ventral to) the corresponding ramus and is inserted at the end of the ramus on the convex ventral surface — *convex root* (Figs. 11, 14, *con.*).

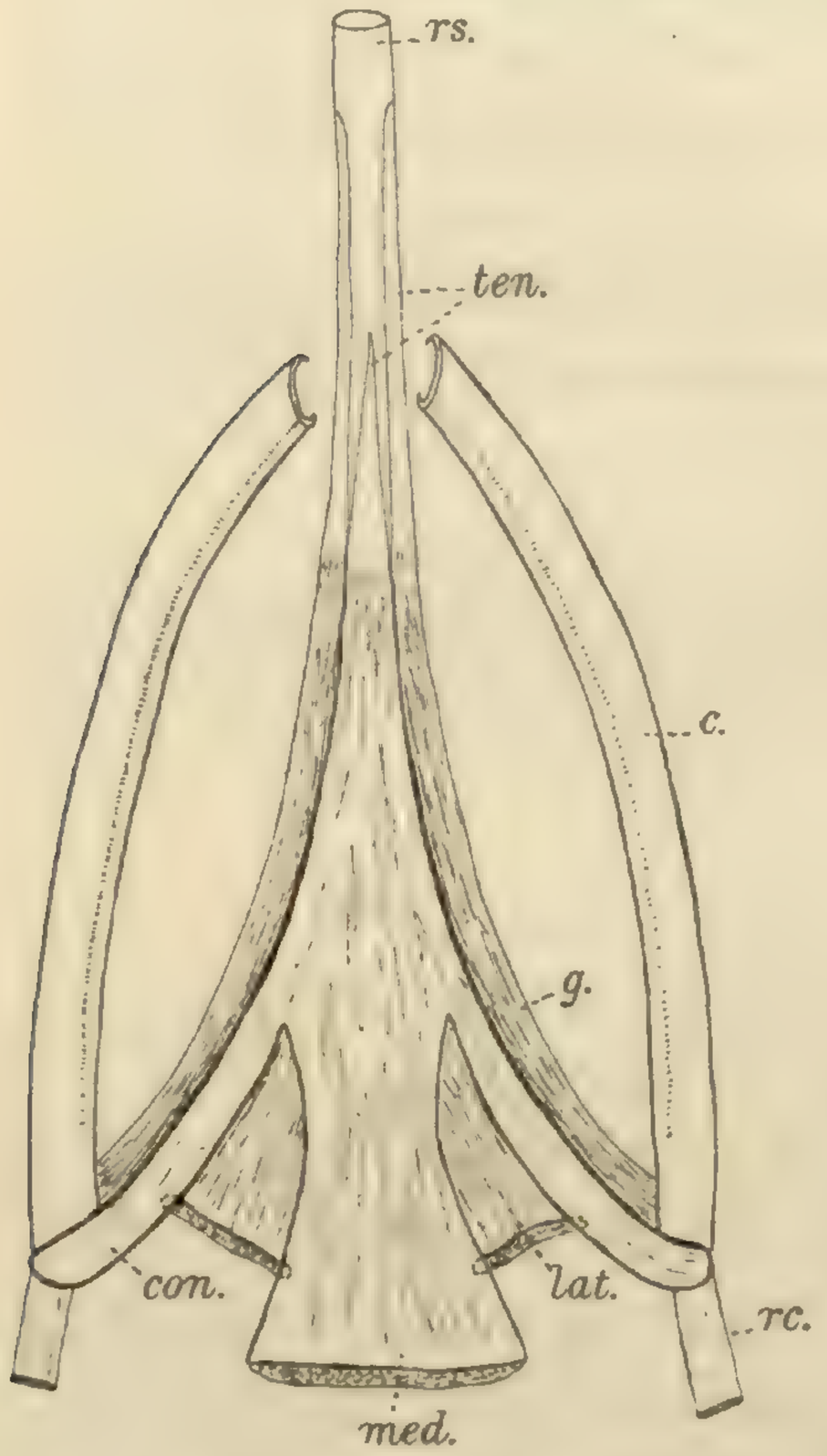

FIG. 14. — *Sycotypus canaliculatus*. Ventral view of the great retractor of the lingual ribbon (semidiagrammatic); the ventral sheet of cross fibers has been removed, its line of attachment, however, is represented; the head of the cartilage has been removed, the rami in part only being shown. *c.*, cartilage, ramus of; *con.*, convex root of great retractor; *g.*, groove root of great retractor; *lat.*, lateral root of great retractor; *med.*, median root of great retractor; *rc.*, retractor of cartilage; *rs.*, radular sac; *ten.*, tendons of origin of great retractor.

Thus the larger part of the *retractor* is inserted into the wall of the proboscis, while the smaller portion finds insertion on the cartilage frame.

As stated, these four roots unite anteriorly to form what may be called the *great retractor of the radula*, which is inserted by one ventral and two lateral tendons into the radular sac (Fig. 14, *ten.*). These tendons and their muscular continuations run in the doubly grooved roadway formed by the grooved dorsal surfaces of the two cartilage rami, these being close together anteriorly, held so by cross fibers that pass between them.

One set of these cross fibers forms what may be called the *ventral sheet of cross fibers*, passing from the convex ventral surface of one ramus to that of the other (Figs. 10, 11, *vscf.*). This sheet extends from the beginning of the rami back to about the place where the dorsal sheet (see further) ends; the ventral sheet ends somewhat anteriorly to the dorsal sheet. In describing the odontophoral cartilage, it will be remembered that mention was made of a line of muscular insertion along the ventral surface of the ramus; this is the line for the insertion of the ventral sheet.

Covering the great retractor are two sets of muscles that call for

attention here, since their purpose is to keep the retractor true to its grooved path. It should be stated in the first place that a considerable portion of the radular sac projects free above the roots of the retractor of the radula, and is continued posteriorly into a rather long *radular muscle* that is inserted into the muscle cup at the base of the proboscis (Fig. 11, *rs.*, *rms.*). The more anterior part of the radular sac has inserted into it laterally and dorsally strands of muscle, some of which pass forward to be inserted into the outer edges of the rami of the odontophoral cartilage; others pass backward to the same edges, thus giving rise to a criss-crossing which serves to keep the radular sac in position and to prevent the great retractor leaving its grooved pathway (Fig. 15).

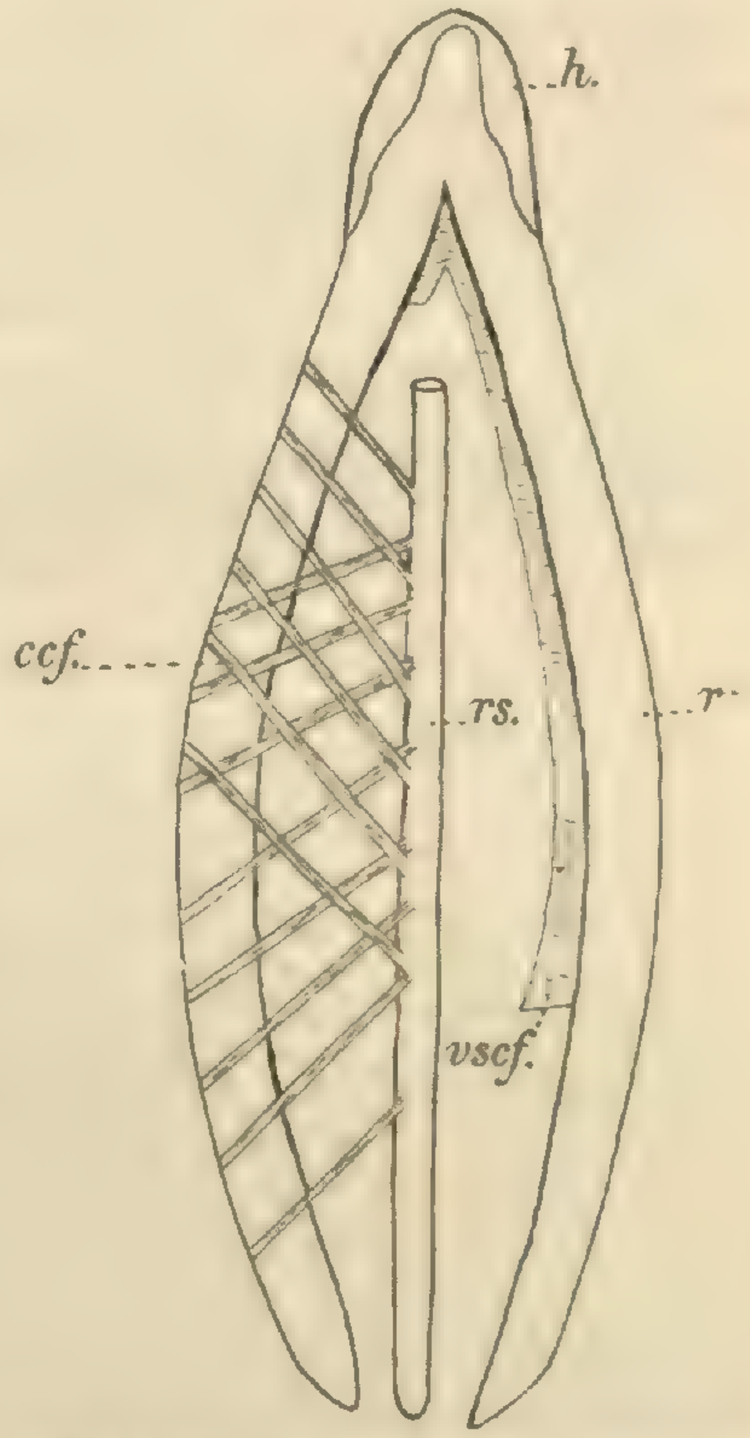

FIG. 15.—*Sycotypus canaliculatus.* Diagrammatic figure to illustrate the criss-cross fibers of the radular sac; the cartilage rami are drawn as spread apart, the ventral sheet of cross fibers having been cut through; one side only of the criss-cross is shown. *ccf.*, criss-cross fibers; *h.*, head of cartilage; *r.*, ramus of cartilage; *rs.*, radular sac; *vscf.*, ventral sheet of cross fibers.

Dorsal to this double set of muscle strands, *i. e.*, more superficial, lies what may be called the *dorsal sheet of cross fibers* (Figs. 9, 11, *dscf.*), which pass from the outer edge of one ramus to the outer edge of the other, not, however, along the entire length of the ramus but to within two cm. or so of the end. This dorsal sheet covers the criss-cross strands and the anterior part of the radular sac, as well as the anterior portion of the great retractor. All that is seen of the great retractor, upon opening the proboscis along the mid-dorsal line and removing the esophagus, is the roots passing from beneath the posterior edge of the dorsal sheet along with the radular sac (Fig. 9).

The dorsal sheet of cross fibers thus serves to keep the rami approximated, and to form a sheath for the radular sac and great retractor, keeping the two in the proper place for motion along the grooved roadway of the rami, therein sharing the function of the

criss-cross strands. Also, the two sheets of cross fibers, dorsal and ventral, serve on contraction to give stiffness to the cartilage frame as a whole and to prevent its buckling.

Nervous Supply of the Great Retractor.—The great retractor muscle is supplied from the stout nerves that leave the buccal ganglia and run forward to penetrate the lateral halves of the median root, and then to continue on to the other roots, and also to the retractors of the cartilage (Fig. 10, *5*).

Protractors.—The protractors of the lingual ribbon are six quite distinct long slender muscles that are found on the ventral side of the buccal mass and of the odontophoral cartilage. There are three on either side of the mid-line (Figs. 10, 11, *prr.*, *a*, *b*, *c*).

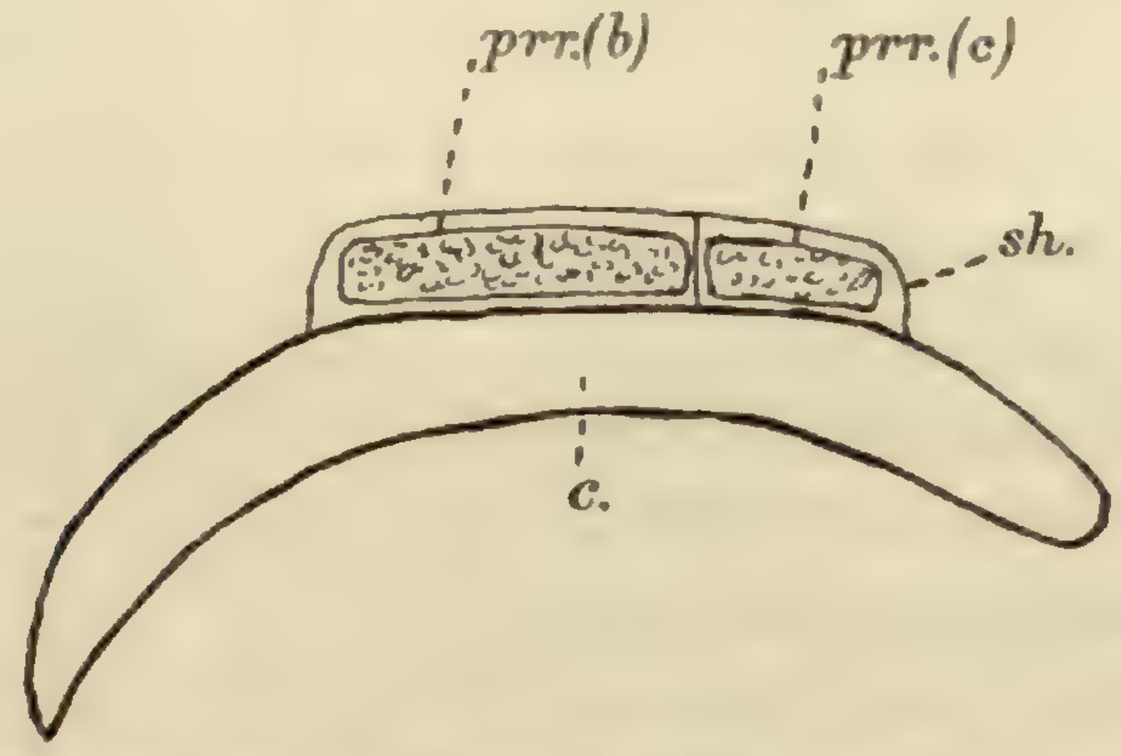

FIG. 16.— *Sycotypus canaliculatus*. Diagram to illustrate the position of the protractors of the radula upon the cartilage ramus. *c.*, cartilage, ramus of; *prr.* (*b*, *c*), protractors of radula; *sh.*, connective tissue sheath.

The protractors arise from the membranous pouch in which the anterior part of the ribbon is found, and extend quite or almost straight backward.

(1) The most ventral muscles are a pair that lie as two delicate red bands along the mid-ventral line of the buccal mass, separated by a white line (blood vessel) (Figs. 10, 11, *prr.*, *a*). They arise from the ventral surface of the membranous pouch, and pass backward, adherent to the ventral sheet of cross fibers, to mingle with the lateral halves of the median root of the great retractor of the radula.

(2) The pair lying more dorsal are the largest — about four times the size of the first pair (Figs. 10, 11, *prr.*, *b*). Each arises from the dorsal surface of the membranous pouch and passes back along the inner half of the ramus of the odontophoral

cartilage on its ventral side in a shallow groove. It is held in place by a sheet of connective tissue that binds it against the ramus, but, at the same time, allows it to slide freely back and forth along the face of the ramus. Each muscle of the pair extends to very near the tip of its ramus, and is there inserted laterally.

(3) The last pair — much smaller than the second but larger than the first pair — arise close to, and laterally from, the second and pass parallel to the second along the outer half of the ramus on its ventral surface to be inserted, a centimeter or so anteriorly to the end of the ramus, into its outer edge (Figs. 10, 11, *prr.*, *c*). The muscles of this pair are, like those of the second pair, contained within a connective-tissue sheath (Fig. 16).

The anterior parts of all these protractors are covered by the cross fibers that pass between the two triangular cartilage protractors (Fig. 11, *cf.*). These three remarkably long muscles (they would make fine material for physiological experiments upon molluscan muscle because of their length and regularity) serve to pull the membranous pouch toward the base of the proboscis, and consequently the lingual ribbon, which is adherent to the inner surface of the dorsal wall of the pouch, out over the head of the odontophoral cartilage. Their mass is extremely small when compared with that of the great retractor, and this is what one would naturally expect, since the rasping takes place on the return pull. It is then that resistance is to be overcome, and there is need for a large muscle, whereas in the forward motion of the lingual ribbon very little power is required, since the teeth of the ribbon have their "set" backward, and merely slip over the surface to be rasped on the forward motion of the ribbon (Fig. 13).

It is very easy to demonstrate the rasping action of the dentate ribbon on a recently narcotized specimen by alternately stimulating the retractor and protractors, when the ribbon plays back and forth very prettily. Of course, the same result is obtained by alternately stimulating the proper nerves, as I have frequently done. It might be well to mention the fact that the nerves of Sycotypus are very slow in dying; they respond to a stimulus (electrical) twenty-four hours and more after the animal has been taken from the alcohol and turpentine mixture.

Nervous Supply.—The protractors of the ribbon are supplied by nerves from the cerebral ganglia. The cords supplying them branch off from the two (one on either side) which go to the protractors of the cartilage. Where one of the latter passes under the first cartilage protractor the cord comes off and, piercing a few of the protractors near their origin, passes on to the surface of the lingual protractors that lie upon the ramus, and then continues on to the ventral sheet of cross fibers, which it supplies, and on to the first pair of slender lingual protractors (Fig. 10, *7*). As will be seen on consulting the figure, a sort of parallelogram anastomosis is formed by this nerve upon the ventral surface of the buccal mass in its lower third.

MUSCULATURE OF THE PROBOSCIS, NERVE SUPPLY

The proboscis wall itself has a very well developed musculature. This musculature is white in contrast to the very red muscles of the buccal mass. The innermost layer of the proboscis wall is one of longitudinal fibers, next comes a tolerably thick circular layer, and beneath the integument is found another longitudinal layer. The contraction of the longitudinal layers serves, of course, to shorten the proboscis and to increase its diameter, whereas the contraction of the circular layer would have the opposite effect.

The innermost longitudinal layer (at least) is supplied by nerve cords that spring from the cerebral ganglion and pass forward along the esophagus piercing in their course the muscle cup at the base of the proboscis. One of these cords passes along outside the line of insertion of the cartilage protractors to the end of the proboscis, giving off branches to the wall of the proboscis as it proceeds (Figs. 5, 10, *4*). Another cord passes along parallel to the one just mentioned, but inside the line of insertion of the protractors of the cartilage (Figs. 5, 10, *3*). Still another, which sometimes, at least, comes off as a branch of the second, passes forward a little farther in toward the mid-line and is covered, like the second in its anterior portion, by muscle strands that pass from the esophagus to the wall of the proboscis.

At the base of the proboscis is situated the muscle cup already mentioned, and which is composed of transverse fibers that mingle

with the musculature of the proboscis wall (Fig. 5, *m. cup*). There is also a *ring muscle* entering into this muscle cup, which surrounds the esophagus, but is free from it on the dorsal, though adherent to it on the ventral side (Fig. 9, *rnm.*).

Below the cup are found very numerous white bundles of muscle which arise, in part, from the cup, from the ring muscle, and also from the proboscis wall with which they are continuous, and, in part, from the fold of integument that surrounds the base of the proboscis (Fig. 2, *rpb.*). These bundles pass backward to mingle with the musculature of the integument that extends back from the head fold to the columellar muscle; some bundles may mingle with the fibers of the columellar muscle.

They serve on contraction to pull the whole proboscis back within the head fold. They might be called the retractors of the proboscis. These retractors are supplied from the cerebral ganglia.

Retraction and Protraction of the Proboscis.

Since there exists a distinct set of retractors at the base of the proboscis, and since its wall has in part a musculature of longitudinal fibers, it is not difficult to understand how retraction is brought about. The basal retractors pull the whole proboscis backward and the longitudinal fibers on contraction shorten it. From dissections made upon specimens with retracted proboscis, it seems that ordinarily there is no turning wrong side out of the proboscis, the shortening of the proboscis itself, and the contraction of the numerous retractors that run into the head fold, together with the flexion of the proboscis, being sufficient to carry the organ altogether back within the head fold. However, a certain amount of doubling wrong side out may — in fact, does — take place under artificial conditions. At the base of the proboscis, there is, as stated, the muscle cup with its ring muscle; between this ring muscle and the esophagus on the dorsal side there exists a space. It is through this free space that the doubling takes place. Into the anterior border of the ring muscle are inserted some of the retractors of the proboscis, and on their contraction that part of the proboscis above the ring begins to double back through the

space left between the ring muscle and the esophagus. On violent stimulation (dissecting an animal that is not well narcotized) this process may be so extensive as to double the whole proboscis within the ring muscle, just as if one were to push in a finger of a glove down to its base. In other words the proboscis may be doubled in on itself down to the place marked *x* in Fig. 2.

This "Einstülpung" must be brought about by the extensive contraction of the retractors of the proboscis and their continuation, the inner longitudinal muscular layer of the proboscis wall. The proboscis cannot be turned wrong side out throughout its entire length, as could a finger of a glove; for in the anterior end the esophagus, which is closely bound to the dorsal wall of the proboscis, and the buccal mass are united. Besides, the protractors of the cartilage prevent such a complete doubling (Fig. 17).

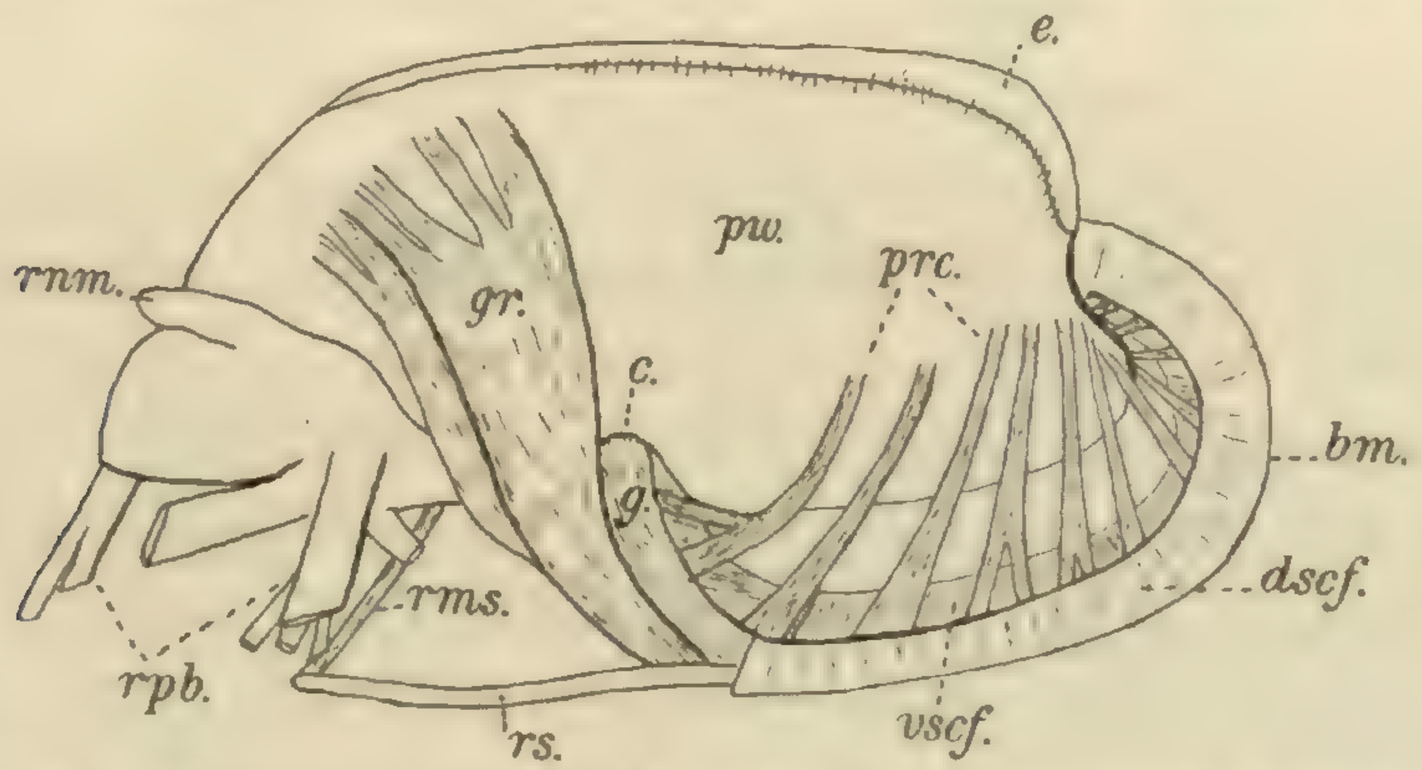

FIG. 17.— *Sycotypus canaliculatus*. Side view of proboscis turned wrong side out: muscles of buccal mass are filled in with fine lines; the musculature of the proboscis and retractors of proboscis are left in outline. *bm.*, buccal mass; *c.*, cartilage, tip of; *dscf.*, dorsal sheet of cross fibers; *e.*, esophagus; *g.*, groove root of great retractor; *gr.*, great retractor; *prc.*, protractors of cartilage; *pw.*, proboscis wall; *rms.*, radular muscle; *rnm.*, ring muscle; *rpb.*, retractors of proboscis; *rs.*, radular sac; *vscf.*, ventral sheet of cross fibers.

As to the protraction of the proboscis, I have only theory to offer, as the experiments which I had contemplated upon this point were never carried out. Of course, the relaxation of the longitudinal fibers, as well as the contraction of the circular fibers of the proboscis wall will account for its elongation, but how is the proboscis forced out of the head fold? It may be that this is done by means of a blood reservoir (sinus) within the head fold. If this be filled with blood, and then the muscles of the head fold contract, the effect would be to expel the proboscis. The region of the head fold that is covered by the collar of the mantle is cavernous,

and if it acts as a blood sinus, there is little difficulty in explaining how the proboscis is pushed out by hydrostatic pressure.

Summary and Conclusion

The results of the present investigation may be summed up as follows: —

The odontophoral apparatus in Sycotypus is highly complex, but admirably adapted to its function.

The mechanism of the radula, in Sycotypus at any rate, is correctly termed, after Huxley, a chain saw, with the restriction that the "sawing" occurs only on the return draw.

The buccal cartilage, besides forming a stiffening framework, acts as a grooved pathway along which the radular sac and the great retractor of the dental ribbon slide, the path being well lubricated, probably by a mucous secretion. In Sycotypus the cartilage is passive, so far as any licking action is concerned. The buccal cartilage possesses its own muscles for protraction and retraction, as well as certain muscles that bind its rami together and at the same time form a sheath for the retractor of the radula.

The radula is protracted, *i. e.*, drawn forward, by six slender muscles, four of which (two pairs) lie along the ventral side of the rami of the buccal cartilage enclosed within connective-tissue sheaths; the other pair lie along the mid-ventral line of the buccal mass. The radula is retracted by a powerful muscle that arises from its sac and is inserted by a number of roots into the proboscis wall and upon the cartilage frame. This inequality of the muscles is explained by the fact that the teeth of the tongue-file are inclined backward, so that the rasping takes place on the return pull.

The retraction of the proboscis is accomplished through its own longitudinal musculature and the continuation of this, the retractors of the proboscis; there is usually little, if any, turning wrong side out of the organ, though this may under certain conditions take place. The protraction of the proboscis is probably due to hydrostatic pressure created in the head fold by the contraction of its musculature.

By dissection and actual observation of the effects produced by electrical stimulation, the nervous supply for the apparatus described has been in large part determined.

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NOTES AND LITERATURE

BIOLOGY

Loeb's Dynamics of Living Matter.[1]— The point of view of Professor Loeb's new book will be surmised by those acquainted with his other writings. Living organisms are to be considered as chemical machines which differ fundamentally from any machines so far created by man in possessing the peculiarities of automatically developing, preserving, and reproducing themselves. In this volume we have an attempt to analyze the strictly biological phenomena of development, self-preservation, and reproduction from a purely physico-chemical point of view.

Inasmuch as the material and the energy of organisms must be supplied by chemical processes, it is only natural that this subject should receive the first attention. Two lectures are therefore devoted to the general chemical and physical problems involved in a study of living matter.

These two lectures are followed by three of particular interest to the physiologist. Hypotheses of muscular contraction and protoplasmic motion and the physical and chemical factors involved in cell division are treated and an entire chapter is devoted to the important subject of the *rôle* of electrolytes in the formation and preservation of living matter, and another to the effect of heat and radiant energy upon living matter.

While these chapters are especially commended to the physiologist, it does not follow that they are lacking in interest to the biologist whose work touches only incidentally upon modern physiology. But to the mind of the reviewer the first six chapters are of more interest to the physiologist while the final six will be read with the keenest interest by the general biologist as well.

In the chapter on tropisms the essential similarity of tropic responses in animals and plants is considered and in so far as possible all are referred to physico-chemical forces. This presents no great difficulty

[1] Loeb, J. *The Dynamics of Living Matter.* Columbia University Biological Series VIII. New York, The MacMillan Company, 1906. 8vo, xi +233 pp., 64 text-figs. $3.00.

in the case of heliotropism, galvanotropism, and chemotropism, but geotropism and stereotropism are more difficult to explain. The relation of the reactions to lines of force and the reason for this relation are made clear. The discussion of the control of the degree and the sense of heliotropic response is especially interesting. The demonstration of the possibility of controlling these reactions by chemical and other means, the apparent uselessness of many of them, and the fact that many could never be used at all in Nature tend to show that they could not have been acquired by way of natural selection.

The chapters on fertilization and heredity will probably be the first to be read by many biologists. Two effects of the entrance of a spermatozoön into an egg must be distinguished. The first is the starting of the process of development, the developmental effects, while the second is the transmission of the paternal qualities to the organism, the hereditary effect. Under the first of these heads are considered the specific character of the fertilizing power of the spermatozoön, and its modification by chemical means — so that forms otherwise incapable of crossings may be hybridized — and the principles and results of experiments in artificial parthenogenesis. While the development of the egg may be caused without the presence of a sperm nucleus or an enucleated fragment of egg protoplasm may be caused to develop by fertilization by a spermatozoön, we must recognize the hereditary effect of egg or sperm nucleus as a distinct phenomenon. The structure of the gametes is exceedingly simple and yet instincts as well as bodily form are transmitted through the sexual cells. Obviously purely morphological conceptions cannot carry us very far here and we first think of definite chemical compounds as the bearers of hereditary qualities. The evidence afforded by experiments upon the toxic effect of the blood of a different species seems significant in this connection but our real knowledge of these phenomena is very meager and it seems impossible to draw any far-reaching inferences.

The minute size of the gametes precludes any extensive analyses of the physico-chemical processes concerned in the formation of organs, but the conditions of morphogenesis may be studied in regenerative processes. Loeb follows Sachs in the view that the variety in the form of organs is determined by a corresponding variety in their chemical constitution and advances arguments from heteromorphosis in various forms. The influence of the central nervous system is discussed and the possibility of the conduction of definite chemical substances to or from the ganglia is suggested.

It is hardly necessary to state that in so far as views on evolution are expressed they are essentially de Vriesian and with the acceptance of the validity of de Vries's conclusions concerning discontinuity, there is the suggestion of the physico-chemical nature of discontinuity in evolutionary transformations.

The Columbia University Biological Series is so familiar to naturalists that comment upon the attractiveness of the volume is quite superfluous and we may simply say that the general scientific public is to be congratulated on having in a condensed form the point of view and chief results of the school of biologists of which Professor Loeb is our best known advocate.

J. A. Harris

ZOÖLOGY

Capture of the Salamander, Autodax lugubris, at Los Angeles, Cal. — One of the points of interest concerning the genus Autodax is its extremely limited range. The taking of a specimen of *A. lugubris* in Los Angeles, Cal., a locality at a considerable distance from what has heretofore been considered the center of its distribution, seems of sufficient importance, therefore, to justify this note on the subject.

In a previous paper on the species by Professor Ritter and myself (*Amer. Nat.*, vol. 33, pp. 691–704, 1899), mention is made of the distribution of the genus as follows: "Autodax is a genus of salamanders confined, according to our present knowledge, to western North America and almost entirely to California." Cope (*U. S. Nat. Mus., bull.* 34) states that "no species has yet been found east of the Pacific coast region." He describes the three species of the genus from specimens in the U. S. National Museum which are distributed as follows:—

16 specimens,		Petaluma, Cal.	Lat. 38° 15′ N.
5	"	Farallone Is.	37° 40′ "
10	"	San Francisco	37° 40′ "
4	"	Berkeley	37° 40′ "
7	"	Monterey	36° 45′ "
1	"	Fort Tejon	35° 0′ "
		Range	3° 15′

A. ferreus, 1 specimen, Ft. Umpqua, Ore.

A. iëcanus, 2 specimens, Baird, Cal., Lat. 40° 50′ N.

The range of *A. iëcanus* was extended by Van Denburgh (*Proc. Cal. Acad. Sci*, n. s., vol. 5, pp. 776–778, 1895) southward to Los Gatos, Cal., Lat. 37° 10′ N. Range, 3° 10′.

Omitting the little known *A. ferreus*, the others of the genus have a range in central California of very narrow limits. Cope sums up the evidence for the better known *A. lugubris* as follows: "The range of this species is limited, embracing only middle California."

The observations of Professor Ritter and myself (*Amer. Nat.*, vol. 33, pp. 691–704, 1899; vol. 37, pp. 883–886, 1903) show its comparative abundance in the whole San Francisco Bay region. In fact, Monterey and Fort Tejon are the only localities outside the bay region from which it has previously been recorded. The remarkable occurrence on the rocky Farallone Island 30 miles off shore was also re-established by a party from the University of California under Professor Torrey in 1903.

The specimen taken in Los Angeles, Lat. 33° 40′ N., extends the range a degree southward thus increasing the previously known range by almost 33%. The occurrence is further striking in that there is a decided climatic difference between this locality and the bay region. The temperature averages of the bay region range from 52° to 60° and those of the Los Angeles region from 60° to 68°. The low average humidity of the Los Angeles region makes this difference even more pronounced. Again, the two localities are separated by barriers of desert and mountain ranges running at right angles to the coast line, a combination of conditions which suffices to isolate several subspecies of birds in the Los Angeles region by checking the north and south diffusion. *A. lugubris* seems, then, to be less timorous than we had at first thought.

The Los Angeles specimen was taken on March 18 of this year, which date is in the midst of the rainy season. The animal was found under a rotten log in just such surroundings as one would expect to find the species in the bay region. The appearance is that of a typical specimen of the third year except that the lemon yellow spots are slightly more numerous than in the majority of specimens from the bay region. Only one specimen was taken but the fact is of minor significance as the species is a bit erratic in its distribution in the bay region.

LOYE HOLMES MILLER

Pimephales notatus in the Lower Susquehanna.— This fish is said to range from Quebec to Delaware and west in the Mississippi valley, thus embracing the above-named river basin where, however, I have not found it recorded before. A number of examples, one a breeding male, was secured by Mr. Witmer Stone and myself while at York Furnace, York Co., Pa., during the middle of May. *Alosa sapidissima, Anguilla chrisypa, Brama creysoleucas, Notropis bifrenatus, N. analostanus, Rhinichthys atronasus, Hybopsis kentuckiensis, Ameiurus nebulosus, Fundulus diaphanus, Lepomis auritus, Eupomotis gibbosus, Perca flavescens, Boleosoma nigrum olmstedi, Plethodon erythronotus, P. glutinosus, Diemyctylus viridescens, D. miniatus, Desmognathus fuscus, Acris gryllus crepitans, Hyla pickeringii, H. versicolor, Rana palustris, R. clamata, R. catesbiana, R. pipiens, Natrix sipedon, Thamnophis sirtalis, Chrysemys picta,* and *Terrapene carolina* were taken, seen, or heard. With the exception of a single small *Exoglossum maxillingua* found in Otter Creek, no fishes were obtained in any of the nearby tributaries, all of which are swift, rocky, and of rapid descent. Besides the above, *Petromyzon marinus, Pomolobus pseudoharengus, Salvelinus fontinalis, Ameiurus catus, Stizostedion vitreum, Roccus americanus, Morone americanus,* and *Cryptobranchus alleganiensis* were reported to occur though we did not see any examples.

HENRY W. FOWLER

Notes.—*Origin of the Vascular Endothelium and of the Blood in Amphibia.*— Kati Marcinowski has attacked this vexed problem, using for his material Siredon and Bufo. His results are summarized as follows (*Jen. Zeitschr.*, vol. 34, 1906):—

The vascular endothelium arises from the mesenchyme and chiefly and possibly exclusively from the secondary mesenchyme. The primary mesenchyme which perhaps contributes, is derived from the ectoderm. No traces were seen of the origin of mesenchyme from the entoderm.

Vascular and blood formation is localized in two regions which in position correspond to the site of the dorsal and ventral mesenteries —sclerotomal and medioventral mesoderm regions. Besides the formation of endothelia from localized anlagen there is also a similar formation from diffusely appearing wandering cells and in connective tissue.

In their first appearance the results are either solid at first and at the first appearance of a lumen are closed to all other cavities or they

are open and connect with other spaces in the mesenchyme or connective tissue. The differences in method of formation are referable to locally different conditions of development and have no important morphological value.

The endothelium arises at a time when the blood corpuscles are in circulation in connection with lacunæ, the schizocœle, in the connective tissue and is to be regarded as arising phylogenetically from a lacunar system bounded by connective tissue whose physiologically most important and hence earliest differentiated portion lay in the region of the gut.

The localization of the blood and vascular forming cells in the region of the mesenteries confirms the view of Lang, founded on comparative anatomy, that the first differentiation of the intestinal blood sinus of the Cœlomata occurred in the separation of vessels in the region of the dorsal and ventral mesenteries.

The blood corpuscles are to be regarded as 'swimming mesenchyme cells' in Ziegler's sense. They arise in the medio-ventral mesoderm region.

J. S. K.

BOTANY

Notes.— The concluding fascicle (parts 5 to 9) of vol. 8 of the *Reports of the Princeton University Expeditions to Patagonia*, which is devoted to an account of the flowering plants by Professor Macloskie, was issued on February 26th. It brings the total pagination for the quarto volume up to 982 and the plates to 31; and in addition to the conclusion of the list of species contains an analysis of orders and families, a list of collectors, with bibliography, an account of the topography of the country, and a chapter on the character and origin of the Patagonian flora.

Vol. 4 of Reiche's *Flora de Chile* completes the Compositæ and contains correction sheets for the first four volumes.

A third "Contribution to the Flora of the Bahama Islands," by Britton, is separately issued from vol. 4 of the *Bulletin of the New York Botanical Garden*, under date of March 19.

Under the title "Prænunciæ Bahamenses," Millspaugh begins a series of contributions to a flora of the Bahaman archipelago, the first part, issued as *Publication 106* of the Field Columbian Museum in February, dealing with Amaranthaceæ, Euphorbiaceæ, Rubiaceæ, Verbenaceæ, and *Solanum didymacanthum.*

A list of pteridophytes and flowering plants collected in Bermuda in 1905 has been privately printed by A. H. Moore, of Cambridge, who describes two species of phanerogams as new.

A local flora of the region readily accessible from Philadelphia has been published by the Botanical Club of that city, and is offered for sale by Mr. Stewardson Brown, who, with Dr. Ida Keller, has edited it.

Talbot is publishing an account of the distribution of the forest flora of the Bombay Presidency and Sind, in current issues of *The Indian Forester.*

A list of pteridophytes and spermatophytes of Delaware County, Pa., is published by Fussell in the *Proceedings of the Delaware County Institute of Science,* of Media, Pa.

An illustrated account of native edible plants, by seasons, is being printed by Rusby in current issues of *Country Life in America.*

A popular guide to the commoner North American trees, intended for the novice and largely illustrated, has been issued by Julia E. Rogers from the press of Doubleday, Page, and Co., of New York.

Volume 1 of de Wildeman's "Etudes de systématique et de géographie botanique sur la flore du Bas et Mayen-Congo" has been completed by the issuance of a third fascicle from the press of the *Musée du Congo* of Brussels. The volume, in quarto, contains 346 pages and 73 plates.

A list of 30 timber trees native to the State, with good bark and wood photograms of each, is given by Douglass in the fifth *Annual Report of the State Board of Forestry of Indiana,*— which contains other interesting papers on the trees of the State and their enemies.

An account of the southern Appalachian forests, by Ayres and Ashe, constitutes *Professional Paper No. 37* of the U. S. Geological Survey.

Lemmon gives a profusely illustrated account of Californian trees in *Out West,* for March.

The *Flora of Tropical Africa*, under the editorship of Sir W. T. Thiselton-Dyer, reaches Buchnera in vol. 4, sect. 2, part 2, recently issued.

An illustrated paper on new American Coralline algæ, by Foslie and Howe, is separately distributed from vol. 4 of the *Bulletin of the New York Botanical Garden.*

An account of the foliaceous and fruticose lichens of the Santa Cruz Peninsula, California, by Herre, forms a brochure of the *Proceedings of the Washington Academy of Sciences* issued on March 29.

A medico-legal study of the spores of the higher fungi is published by Offner in vol. 34 of the *Bulletin de la Société de Statistique. . . .de l'Isère.*

A thesis on the nature and origin of the binucleated cells in some Basidiomycetes, by Susie P. Nichols, is separately issued from vol. 15 of the *Transactions of the Wisconsin Academy of Sciences, Arts, and Letters.*

The morphology of Gymnosporangium galls forms the subject of a paper by de Lamarlière in the *Annales des Sciences Naturelles, Botanique,* of March.

A further contribution to the literature of sexuality in Uredineæ is made by Blackman and Fraser in the *Annals of Botany* for January.

An extensive paper on the origin and distribution of rust diseases is contributed by Eriksson to the *Arkiv för Botanik*, vol. 5, parts 1–2.

An economic account of *Glomerella rufomaculans*, by Scott, forms *Bulletin no. 93* of the Bureau of Plant Industry, U. S. Department of Agriculture.

Rehm continues his descriptions of North American Ascomycetes in *Annales Mycologici.*

A paper on new or rare Pyrenomyceteæ from western New York, by Fairman, forms a brochure of the *Proceedings of the Rochester Academy of Science,* issued in March.

The fungi of Camembert and Roquefort cheese, from which *Penicillium camemberti* and *P. roqueforti* are described and figured as new, are discussed by Thom in *Bulletin no. 82* of the Bureau of Animal Industry, U. S. Department of Agriculture.

Thaxter's group of Myxobacteria is the subject of an extensive illustrated article by Quehl in the *Centralblatt für Bakteriologie*, etc., 2 Abteilung, of March 6.

The deterioration of commercial cultures for legumes is noted in *Bulletin no. 270* of the New York Agricultural Experiment Station.

An account of *Bacillus necrophorus* and its economic importance, by Mohler and Morse, forms *Circular no. 91* of the Bureau of Animal Industry, U. S. Department of Agriculture.

A further discussion of the effect of drying upon the bacteria of leguminous root tubercles is contributed by Kellerman and Beckwith to *Science* of March 23.

A paper on the bacterial flora of the city water of Madrid is published by Madrid Moreno as vol. 3, no. 2, of the *Memorias de la Real Sociedad Española de Historia Natural.*

Bacillus nicotianæ, causing a wilt disease of tobacco, is described by Uyeda in vol. 1, no. 1, of the *Bulletin of the Imperial Central Agricultural Experiment Station of Japan*, issued in December last.

A new presentation of Myrmecophily, with interesting illustrations, is given by Ule in Engler's *Botanische Jahrbücher* of February 27.

A recent number of the *Allgemeine botanische Zeitschrift* notes that in the Königsberg district a fine of 150 Marks has been recently prescribed as the penalty for each offense, as a means of stopping the extermination of a rare plant — *Eryngium maritimum.*

The second part of Wittrock's "Catalogus Illustratus Iconothecæ Botanicæ Horti Bergiani Stockholmiensis," constituting vol. 3, no. 3, of the *Acta Horti Bergiani*, is a thick volume with 151 plates of portraits.

A sketch of Woronin's life, with portrait and bibliography, is contained in a recently issued fascicle of the *Travaux du Musée Botanique de l'Académie Impériale des Sciences de St. Pétersbourg.*

A further "coöperative memoir" on inheritance in the Shirley poppies, with a color plate of petals, is published in *Biometrika* for March.

An account of some of the old herbaria and books of Cassel is given by Schelenz in no. 49 of the *Abhandlungen und Bericht des Vereins für Naturkunde zu Cassel.*

The dedication of more than one genus to a given individual is the subject of protest by Greene in a signature of his *Leaflets* issued on April 10.

Osterhout publishes papers on osmotic and toxic questions in a brochure of the *University of California Publications, Botany,* issued on March 13.

"The Vital Fabric of Descent" is the title of a further presentation of his kinetic theory of evolution, by O. F. Cook, in a brochure of *Proceedings of the Washington Academy of Sciences,* issued on March 19.

A posthumous paper by Songeon on the mode of development of the vegetative organs of a large number of the plants of Savoy is published in vol. 10 of the second series of the *Bulletin de la Société d'Histoire Naturelle de Savoie.*

A note on protective resemblances in Mesembryanthemum and Anacampseros, by Thiselton-Dyer, is published in the *Annals of Botany* for April, with good illustrations which, however, are mutilated by the method of insertion in the journal.

A popular lecture on the sensitiveness of plants is separately issued by Kny from vol. 20 of the *Naturwissenschaftliche Wochenschrift.*

Recent studies of the reduction division in the sexual nuclei of plants are summarized by Agnes Robertson in the opening number for 1906 of *The New Phytologist.*

A handbook of plant-breeding applied to a number of important crops, by Fruwirth, is being issued from the Parey press of Berlin.

Rubber culture in Mexico is the subject of an illustrated article by Main in *The American Inventor* for April.

An anatomical study of some plants which yield gutta-percha is being published by Charlier in current issues of the *Journal de Botanique.*

A readable illustrated article on the plant introduction work of the national Department of Agriculture, by Fairchild, appears in *The National Geographic Magazine* for April.

Some sensible ideas on high-school teaching of biology are given by Elma Chandler in *School Science and Mathematics* for May.

Extensive segregation and nomenclatorial revision in a number of groups of phanerogams are contained in recently issued signatures of Professor Greene's *Leaflets*.

Hefte 23 (Halorrhagaceæ, by Schindler) and 24 (Aponogetonaceæ, by Krause and Engler) of Engler's *Das Pflanzenreich* have been issued recently from the Engelmann press of Leipzig.

An account is given by Graebener, in the *Mitteilungen der deutschen dendrologischen Gesellschaft* for 1905, of the Magnolias found hardy in Germany, and is accompanied by a distributional map for those native to the United States. A garden account of the same genus is also published by Miller in *The Garden Magazine* for June.

A revision of the American species of Parthenocissus is published by Rehder in *Mitteilungen der deutschen dendrologischen Gesellschaft* for 1905, which also includes an account of Cercocarpus, by Schneider.

A number of new American species of Ribes are described in the second and third parts of Janczewski's revision of the genus, separately issued in January and May from the *Bulletin International de l'Académie des Sciences de Cracovie*.

A new Burmese species of Eugenia is described and figured by Gage in *The Indian Forester* for January.

A paper on alfalfa seed and its adulterants and impurities, by Roberts and Freeman, forms *Bulletin no. 133* of the Kansas State Agricultural College.

White publishes an account of Robinia and its enemies in *The Popular Science Monthly* for March.

Rubus flavinanus and *R. grontianus* are described from Vermont, as new, by Blanchard in *The American Botanist* of April and May.

A note by Ellwanger on *Cratægus ellwangeriana*, with illustration, is published in *Gardening Illustrated* of May 5.

Four new cacti from Mexico are described by Roland-Gosselin in vol. 11, no. 6, of the *Bulletin du Muséum d'Histoire Naturelle* of Paris.

A second part of Burgess' "Studies in the History and Variation of Asters," dealing with the group Biotia and containing a general discussion of variability in the genus, forms vol. 13 of the *Memoirs of the Torrey Botanical Club*, issued on March 15.

Anatomical studies of Valerianaceæ are published by Vidal in vol. 34 of the *Bulletin de la Société de Statistique . . . . de l'Isère.*

Contrasting seed-figures of *Catalpa speciosa* and *C. bignonioides* are given in *Arboriculture* for May.

The Nepenthes of Madagascar and New Caledonia are revised by Dubard in no. 1 of the *Bulletin du Muséum d'Histoire Naturelle* of Paris, for 1906.

Courchet has a paper on the morphology and anatomy of *Eperua falcata* in the *Annales de l'Institut Colonial de Marseille,* of 1905.

A morphological-anatomical study of Hura is contributed by Gilles to the 1905 *Annales de l'Institut Colonial de Marseille.*

A volume of nearly 100 drawings by W. H. Gibson, with descriptive text by Helena Leeming Jelliffe, is published by Doubleday, Page, and Co., under the title *Our Native Orchids.* Like all of Gibson's work it is sketchy and calculated to stimulate interest in the subjects depicted.

An account of the different sarsaparillas of commerce — without determinations of the species of Smilax that furnish them — is given by Henry in vol. 14, no. 2, of the *Bulletin de la Société Scientifique et Médicale de l'Ouest.*

Habit and trunk pictures of *Ficus benghalensis* are given in *Forest Leaves* for April.

An account of his hybrids of *Yucca flaccida, Y. filamentosa,* and *Y. treculeana* with other species of the genus is given by Sprenger in recent issues of the *Bullettino della R. Società Toscana di Orticultura.*

The North American species of Festuca are revised by Piper in vol. 10, part 1, of *Contributions from the U. S. National Herbarium,* dated March 30.

An economic account of *Allium vineale* as a wheat weed is given by Duvel in *Bulletin no. 100* of the Bureau of Plant Industry, U. S. Department of Agriculture.

A very broad-leaved cultivated form of Hesperoyucca is described in the *Gardeners' Chronicle* of March 10 under the name *Yucca nitida* Wright MS.

An extensive paper on the comparative anatomy and phylogeny of Cyperaceæ is published by Plowman in the *Annals of Botany* for January.

A list of Ottawa Eriophorums is given by Macoun in *The Ottawa Naturalist* for May.

Papers on Calamagrostis, by Forges and Lehbert, with spikelet illustrations, are contained in the *Mitteilungen des thüringischen botanischen Vereins*, n. f., heft 20.

Enzyme-poison production in Zea is noted by Price in *Circular no. 84* of the Bureau of Animal Industry, U. S. Department of Agriculture.

An account of the poisoning of horses in South Africa by *Ornithogalum thyrsoides* is given by Hutcheon in the *Agricultural Journal of the Cape of Good Hope* for February; and Delphinium and other stock-poisoning plants of Colorado form the subject of *Bulletin 113* of the Experiment Station of that State, by Glover.

The natural replacement of *Pinus strobus* in old fields in New England is the subject of *Bulletin no. 63*, Bureau of Forestry, U. S. Department of Agriculture, by Spring.

A practical little book on *Ferns and How to Grow Them*, by Woolson, has been issued from the Doubleday Page press of New York.

A new segregate of the *ternatum* group of Botrychium is published by Maxon, under the name *B. alabamense* in a leaflet of the *Proceedings of the Biological Society of Washington*, issued on February 26.

Léveillé notes the occurrence of *Azolla caroliniana* in China, in the February-March fascicle of the *Bulletin de l'Académie Internationale de Géographie Botanique.*

The Journals.— *Botanical Gazette*, February: — Fulton, "Chemotropism of Fungi"; Lewis, "The Embryology and Development of *Riccia lutescens* and *Riccia crystallina*"; Livingston, "Note on the Relation Between Growth of Roots and of Tops in Wheat."

Botanical Gazette, March: — Simons, "A Morphological Study of *Sargassum filipendula*"; Schaffner, "Chromosome Reduction in the Microsporocytes of *Lilium tigrinum*"; Olive, "Cytological Studies on the Entomophthoreæ — I"; Ganong, "New Normal Appliances for Use in Plant Physiology — III."

Botanical Gazette, April: — Olive, "Cytological Studies on the Entomophthoreæ — II"; Spalding, "Biological Relations of Desert Shrubs — II"; Eastwood, "New Species of Californian Plants"; Hitchcock, "Notes on North American Grasses — VI."

The Bryologist, March: — Fink, "Further Notes on Cladonias — VI"; Grout, "Additions to the Bryophyte Flora of Long Island"; Holzinger, "*Grimmia glauca* — a New Species or a Hybrid"; Howe, "*Ramalina rigida* on the Rhode Island Coast"; Hill, "*Encalypta procera* — a Correction"; Watts, "Australian Mosses — Some Locality Pictures."

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Bulletin of the Southern California Academy of Sciences, December, 1905: — P[arish], "*Cereus giganteus* in California"; Hasse, "A Few Lichens picked up on San Jacinto Mountain"; Parish, "A Preliminary Synopsis of the Southern California Cyperaceæ — VIII."

Bulletin of the Southern California Academy of Sciences, March: — Davidson, "A Revision of the Western Mentzelias"; Parish, "A Preliminary Synopsis of the Southern California Cyperaceæ — XI"; Grant, "Wheelerella."

Bulletin of the Torrey Botanical Club, February: —Selby, "Studies in Etiolation"; Kraemer, "Studies on Color in Plants"; Randolph, "The Influence of Moisture upon the Formation of Roots by Cuttings of Ivy"; Underwood and Lloyd, "The Species of Lycopodium of the American Tropics."

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Bulletin of the Torrey Botanical Club, April: — Peck, "New Species of Fungi"; Harris, "The Anomalous Anther-Structure of Dicorynia, Duparquetia, and Strumpfia"; Harper, "Some New or Otherwise Noteworthy Plants from the Coastal Plain of Georgia"; Stockard, "Cytological Changes accompanying Secretion in the Nectar-Glands of *Vicia faba*."

The Fern Bulletin, January: — Bissell, "The Fern Flora of Connecticut"; Davenport, "*Botrychium matricariæfolium*"; Durand,

"Sporangial Trichomes"; Clute, "Tropical Ferns in Southern States"; Hazen, "*Dryopteris filix-mas* in Vt."

The Fern Bulletin, April: — Gilbert, "*Polypodium vulgare* and its Varieties in America"; Rooney, "The Resting of Botrychium"; Clute, "The Forms of the Cinnamon Fern"; Dukes, "An Alabama Station for *Botrychium biternatum*"; Clute, "The Author Citation"; Winslow, "The Distribution of Botrychia"; Clute, "*Polypodium piloselloides*."

Journal of Mycology, January: — Morgan, "North American Species of Marasmius" (*continued*); Kellerman, "Uredineous Culture Experiments with *Puccinia sorghi*, 1905"; Arthur, "Cultures of Uredineæ in 1905"; Durand, "*Peziza fusicarpa* Ger. and *Peziza semitosta* B. & C."; Kellerman, "Notes from Mycological Literature — XVII."

Journal of the New York Botanical Garden, February: — Nash, "Notes from the Conservatories"; Wilson, "The American Dragon's Blood Tree."

Journal of the New York Botanical Garden, March: — Nash, "A Guide to the Conservatories."

Journal of the New York Botanical Garden, April: — Robinson, "The History of Botany in the Philippine Islands"; Rusby, "A Floating Orchid (*Habenaria repens*)"; Hollick, "The Type of *Zamites montanensis* Font."

Muhlenbergia, vol. 1, no. 8 (April, 1906): — House, "Nomenclatorial Changes in the Orchidaceæ"; House, "A New Species of Dichondra"; [Heller], "Western Species, New and Old — V."

Ohio Naturalist, February: — Schaffner, "Check List of Ohio Trees"; Sumstine, "Notes on *Anthurus borealis*"; Schaffner, "Sexual and Nonsexual Generations."

Ohio Naturalist, March: — Fischer, "New and Rare Ohio Plants"; Moseley, "The Cause of Trembles in Cattle, Sheep and Horses, and of Milk-sickness in People" (*continued*); Schaffner, "The Life Cycle of a Homosporous Pteridophyte"; Jennings, "Some New or Noteworthy Species Reported for Ohio in Recent Botanical Literature"; McOwen, "Key to Ohio Catalpas in Winter Condition."

Ohio Naturalist, April: — Fischer, "Ecological Observations on the Flora of the Shale Bluffs in the Vicinity of Columbus, O."; Claassen, "Corrections to the Key to Liverworts"; Schaffner, "Win-

ter Buds of Ohio Trees and Shrubs"; Van Hock, "*Aschochyta pisi* — a Disease of Seed Peas"; Schaffner, "The Classification of Plants — III"; Morse, "Key to Ohio Alders in Winter Condition"; Stockberger, "Further Notes on *Anthurus borealis*."

[*Publication*] *no. 35* of the Manila Bureau of Government Laboratories, issued on January 17, contains part 4 of Merrill's "New or Noteworthy Philippine Plants," "Notes on Cuming's Philippine Plants" by the same author, "Notes on Philippine Grasses" by Hackel, Scitamineæ by Ridley, and Acanthaceæ by Clarke.

The opening numbers of *The Philippine Journal of Science* contain several papers on Cocos.

Plant World, January: — Hitchcock, "Twigs of Woody Plants"; Livingston, "A Simple Method for Experiments with Water Cultures"; Van Hook, "The Hop-hornbeam or Ironwood"; Whittlesey, "The Devil's Tongue."

Plant World, February: — Wiegand, "The Occurrence of Ice in Plant Tissue"; Taylor, "The Georgia Bark or Quinine Tree (*Pinckneya pubens*)"; Koch, "Floral Notes of Foreign Lands."

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Rhodora, March: — Brainerd, "Hybridism in the Genus Viola — III"; Andrews, "Preliminary Lists of New England Plants — XVIII, Sphagnaceæ"; Knight, "Some Noteworthy Plants of the Penobscot Valley"; Riddle, "Contributions to the Cytology of the Entomophthoraceæ — Preliminary Communication"; Smith, "A New Station for *Asplenium ebenoides*."

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Transactions of the American Microscopical Society, vol. 26: — Burrill, "Micro-organisms of the Soil and Human Welfare"; Clements, "Relation of Leaf-Structure to Physical Factors"; Bessey, "Structure and Classification of the Lower Green Algæ."

Transactions of the Kansas Academy of Science, vol. 20, part 1: — Coppedge, "The Effect of Light on *Melilotus alba*"; Sayre, "The Botanical Features of the New United States Pharmacopœia"; Meeker, "A Little Experiment in Flower Making"; Reagan, "Notes on the Flora of the Rosebud Indian Reservation, South Dakota."

Report of the Michigan Academy of Science, vol. 7: — Beal, "Vitality of Seeds"; Dandeno, "'Color' Stimulus and Vital Functions of Plants"; Bach, "Toxic Action of Copper Sulphate upon Certain Algæ in the Presence of Foreign Substances"; Loew, "A Study of the Effects of Dilute Solutions of Hydrochloric Acid upon the Radicles of Corn Seedlings"; Pollock, "Notes on *Ganoderma sessile*"; "A Canker of the Yellow Birch and a Nectria Associated with it"; "A Species of Hormodendrum on Araucaria"; Pollock and Kauffman, "Michigan Fungi"; Stearns, "A Study of Plants in Ravines near Adrian"; Transeau, "Climatic Centers and Centers of Plant Distribution"; Bretz, "Winter Field Work in Botany"; Levy, "Anthrax-like Bacilli."

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CONTENTS

		Page
I. Variation in the Number of Seeds of the Lotus . .	DR. RAYMOND PEARL	757
II. The Causes of Extinction of Mammalia . . .	PROFESSOR H. F. OSBORN	767
III. A Preliminary Study of the Finer Structure of Arcella	J. A. CUSHMAN and W. P. HENDERSON	797
IV. Notes and Literature: *Astronomy and Physics*, Willson's Laboratory Astronomy, Sabine's Laboratory Physics; *Biology*, Clements's Research Methods in Ecology, Moore's Universal Kinship; *Zoölogy*, Pratt's Vertebrate Zoölogy, Stephens's California Mammals, Ichthyological Notes; *Botany*, Clements on Leaf Structure, Wiesner on Light Intensity, Bilancioni's Dictionary, Notes, The Journals		803

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VARIATION IN THE NUMBER OF SEEDS OF THE LOTUS

RAYMOND PEARL

IN HIS *Mutationstheorie* (vol. 1, p. 112) de Vries puts at the head of a list of topics for further investigation by the student of variation the following sentence: "Das Quetelet'sche Gesetz bedarf immer weiterer Beispiele; die Zahl dieser kann nie gross genug werden." In view of this statement from so distinguished an investigator of the problems of evolution, I venture to publish some material on variation in Nelumbium which has been in my notes for some years and which has frequently been used as an illustration in classroom lectures in biometry. As will be seen in what follows, this material conforms very closely to the normal or Gaussian law in the distribution of its variates; much more closely in point of fact than do many cases which have commonly been cited as typical illustrations of that law.

In marshy situations at many points about the shores of the western part of Lake Erie the common lotus, *Nelumbium luteum* Willd., grows in great abundance.[1] Especially in a strip of water known locally as "Black Channel," which connects Sandusky Bay with the lake, does this plant flourish. Many acres of water are literally covered with its leaves. Pieters (*loc. cit.*, p. 66) says of the growth of Nelumbium in this region: "The immense yellow flowers rising just above the great dark-green standing leaves and the water covered with huge floating pads make this the most striking formation of the swamp. The Nelumbium grows in from

[1] *Cf.* Pieters, A. J. "The Plants of Western Lake Erie, with Observations on their Distribution." *Bull. U. S. Fish Comm. 1901*, pp. 57–79.

2 to 4 feet of water, or stray plants may be found in less than 2 feet. Many of the floating leaves were 20 to 24 inches across and the standing ones not much smaller. At Upper Sandusky Bay I found a floating leaf 26 inches in diameter and another with a petiole more than 5 feet in length. Both at Sandusky Bay and along the Portage River the acreage of Nelumbium was greater than at East Harbor, but nowhere did the plants present a more vigorous growth or so magnificent an appearance."

The large ovoid seeds of this plant are borne in pockets scattered

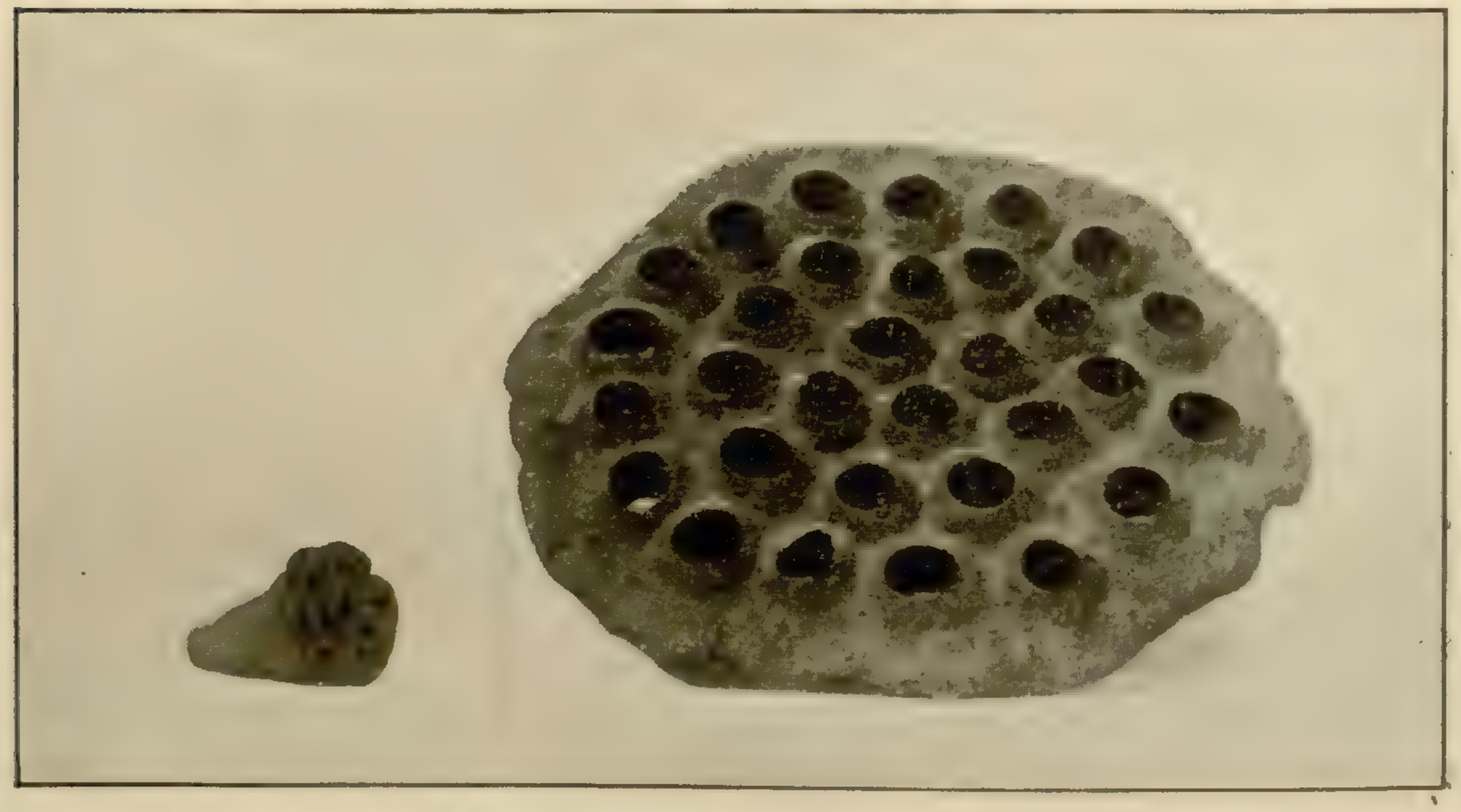

FIG. 1.— Showing the general form of the capsule and arrangement of the seeds in Nelumbium. The two capsules shown in this photograph represent the extremes of variation in the sample; the capsule on the left bore 9 seeds, and the one on the right 39. In the photograph both are reduced below actual size to the same degree.

over the flat, upper surface of the conical seed capsule. After the flower has been shed the ends of the seeds are seen projecting from these pockets. The form of the capsule and the arrangement of the seeds are shown in the accompanying photographs (Figs. 1, 2, and 3), for the preparation of which I am indebted to Miss Frances J. Dunbar.

It is the purpose of the present paper to set forth the results of a study of the variation in the number of seeds to the flower (or the capsule) in this plant. At the end of the flowering season in the summer of 1902 a series of 1410 seed capsules was collected at random from the Black Channel fields in Sandusky Bay. A

count was made of the number of seeds in each of these capsules and the records so obtained form the basis of this paper.

The raw data are exhibited in Table 1.

TABLE 1

Frequency Distribution of Number of Seeds in Nelumbium

Number of Seeds per Capsule	Frequency	Number of Seeds per Capsule	Frequency	Number of Seeds per Capsule	Frequency
9	1	20	60	31	45
10	0	21	101	32	34
11	0	22	111	33	21
12	2	23	113	34	13
13	2	24	114	35	11
14	1	25	107	36	7
15	13	26	137	37	2
16	11	27	120	38	1
17	30	28	101	39	1
18	41	29	90		
19	58	30	62	Total	1410

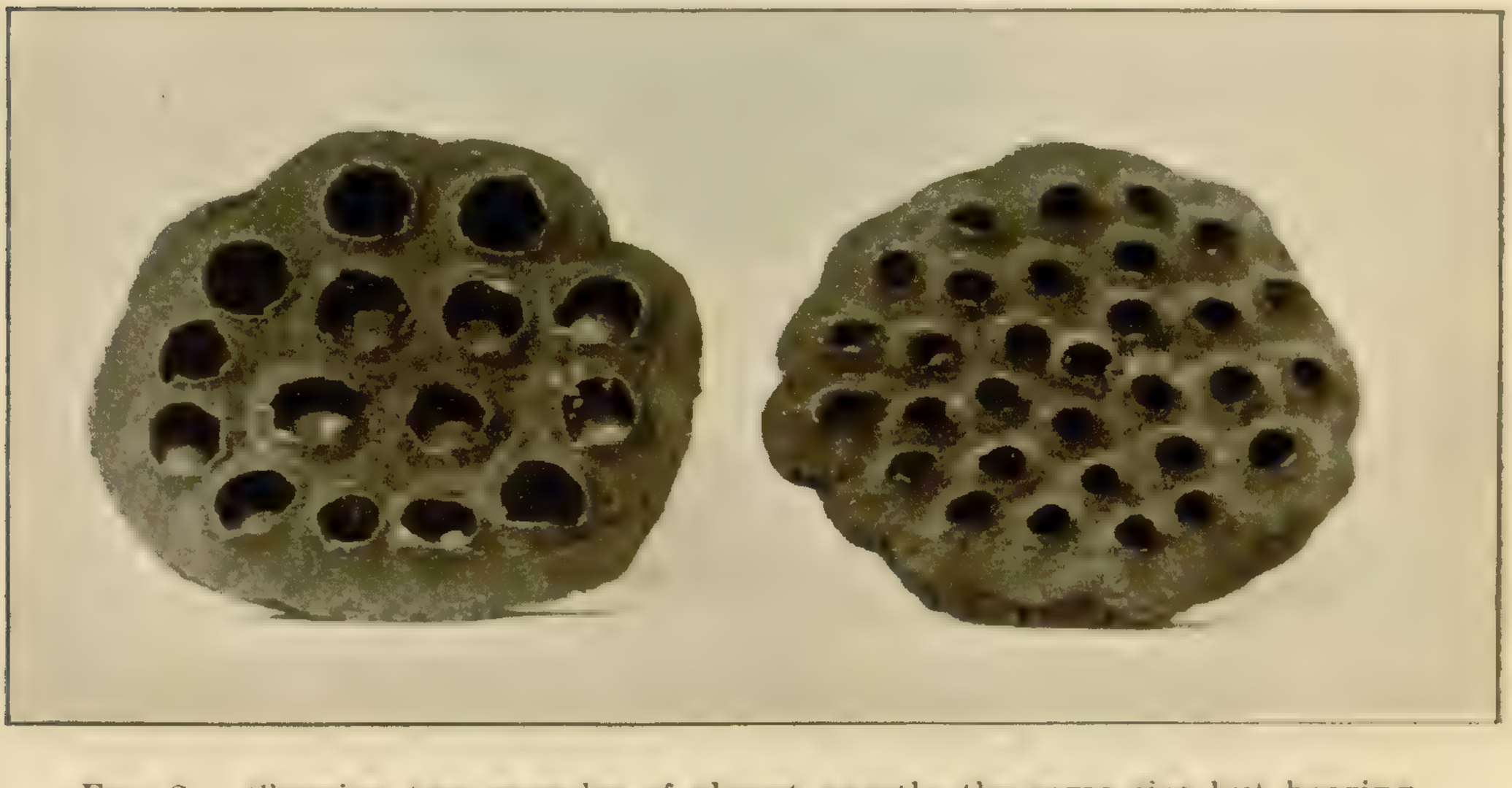

FIG. 2.— Showing two capsules of almost exactly the same size but bearing widely different numbers of seeds, the one on the left having 15 seeds while the other has 31. It should be noted that the openings of the seed pockets have been enlarged with a knife in the specimen on the left. The normal aspect of the capsule top is shown in the right-hand specimen.

The chief physical constants for this distribution are given in Table 2.

TABLE 2

Constants for Variation in Seed Number in Nelumbium

Mean	24.874 ± .078
Standard Deviation	4.339 ± .055
Coëfficient of Variation	17.445 ± .162

It will be noted that the distribution as a whole is quite symmetrical. The relative variability, as measured by the coëfficient of variation, is of the same general order of magnitude as has been found

FIG. 3.— A large, fully developed capsule seen from the side.

in plant characters by other workers. In order to determine whether or not the variation of the character under consideration follows the normal law within the limits of the errors of random sampling we must examine the values of the analytical constants, which define the character of a frequency distribution, in comparison with their probable errors. Using Sheppard's corrections for the moments I find the values given in Table 3. The unit for the moments is 1 seed.

TABLE 3

Analytical Constants for Variation in Nelumbium

Constant	Value
μ_2	18.8307
μ_3	2.4675
μ_4	1022.5949
β_1	0.0009
$\sqrt{\beta_1}$	0.0302
β_2	2.8838
β_2-3	—0.1162
κ_1	—0.2351
κ_2	—0.0029
Skewness	0.0164
Modal Divergence	0.0712
Standard Deviation	4.3394
Mean	24.8745
Mode	24.8033

Further, we have the following values for the probable errors of the chief constants concerned in testing whether the distribution sensibly deviates from the normal law. It will be understood that these are the values of the probable errors for the normal curve.

Probable error of skewness = ± 0.0220
" " " $\sqrt{\beta_1}$ = ± 0.0440
" " " β_2 = ± 0.0880
" " " modal divergence = ± 0.0955

We see at once that neither the skewness, the difference between the mean and the mode, nor $\sqrt{\beta_1}$, are sensibly different from what they would be for an absolutely normal distribution. In the case of each of these constants the theoretical value for a normal curve is zero. The values found from the actual statistics in this reasonably large sample differ from zero by less than the probable errors. Hence we may conclude that in respect to number of seeds per capsule Nelumbium varies symmetrically about the mean (which of course coincides with the modal) condition. A half of the capsules bear less than the typical number of seeds, and a half more than the typical number. Turning to the quantity β_2-3, which measures the degree of flatness at the top of the curve, or, as it has been called

by Pearson,[1] the *kurtosis*, the case is somewhat different. Theoretically the normal curve is mesokurtic, or $\beta_2 - 3 = 0$. Now in the present case $\beta_2 - 3$ differs from zero by more than its probable error. The deviation is less than twice the probable error of β_2, so cannot be considered as significant on this basis. As we shall see, however, we get a somewhat better fit to the data given by the *actual sample* if we use a curve which takes into account this deviation from the mesokurtic condition of the normal curve. In so far, however, as we may infer from the sample regarding the conditions in the general population from which the sample is taken, we can conclude with a high degree of probability that *in the variation in number of seeds per capsule Nelumbium follows the normal law of errors.*

From the values of κ_1 and κ_2 given in Table 3 we see that whatever deviation from normality exists, is in the direction of a curve of Type 1. In order to compare the graduation given by a normal and a skew curve, I have fitted both types of curve to the data. The equation to the normal curve is

$$y = 129.6271\ e^{-\frac{x^2}{37.6614}}$$

while the equation to the Type 1 curve is

$$y = 127.6421\ (1 + \tfrac{x}{28.7285})^{21.7365}\ (1 - \tfrac{x}{32.1508})^{24.3259}.$$

Calculating out the ordinates of these two curves corresponding to the different numbers of seeds, we have the results shown in Table 4.

TABLE 4

Comparison of Observations and Fitted Curves

Number of Seeds per Capsule	Observed Frequency	Ordinates of Normal Curve	Ordinates of Type 1 Curve
9	1	.2	.06
10	0	4	.2
11	0	8	.5
12	2	1.6	1.2
13	2	3.1	2.6
14	1	5.6	5.2

[1] *Biometrika*, vol. 4, p. 173.

TABLE 4 (*continued*)

Number of Seeds per Capsule	Observed Frequency	Ordinates of Normal Curve	Ordinates of Type 1 Curve
15	13	9.7	9.5
16	11	16.0	16.2
17	30	25.0	25.7
18	41	37.0	38.3
19	58	51.8	53.6
20	60	69.0	70.8
21	101	87.0	88.4
22	111	104.1	104.7
23	113	118.1	117.7
24	114	127.0	125.6
25	107	129.6	127.4
26	137	125.3	123.3
27	120	115.0	113.3
28	101	100.0	99.0
29	90	82.5	82.3
30	62	64.5	65.0
31	45	47.9	48.7
32	34	33.7	34.6
33	21	22.5	23.2
34	13	14.2	14.7
35	11	8.5	8.8
36	7	4.9	4.9
37	2	2.6	2.6
38	1	1.3	1.2
39	1	.7	.6

Of course to get absolute accuracy, areas instead of ordinates should be compared with the observed frequencies, but inasmuch as the number of groups is here large, the error made by comparing ordinates will not be serious.

The frequency polygon and fitted curves are shown in Fig. 4.

The fit is seen to be excellent in the case of both the curves, but the slight superiority of the Type 1 curve is apparent. The difference, as has been pointed out above (p. 762), between this and the normal curve is not significant. The greatest discrepancy between the observations and the curves is in the region about the mode. I am unable to account for the curious irregularity in the

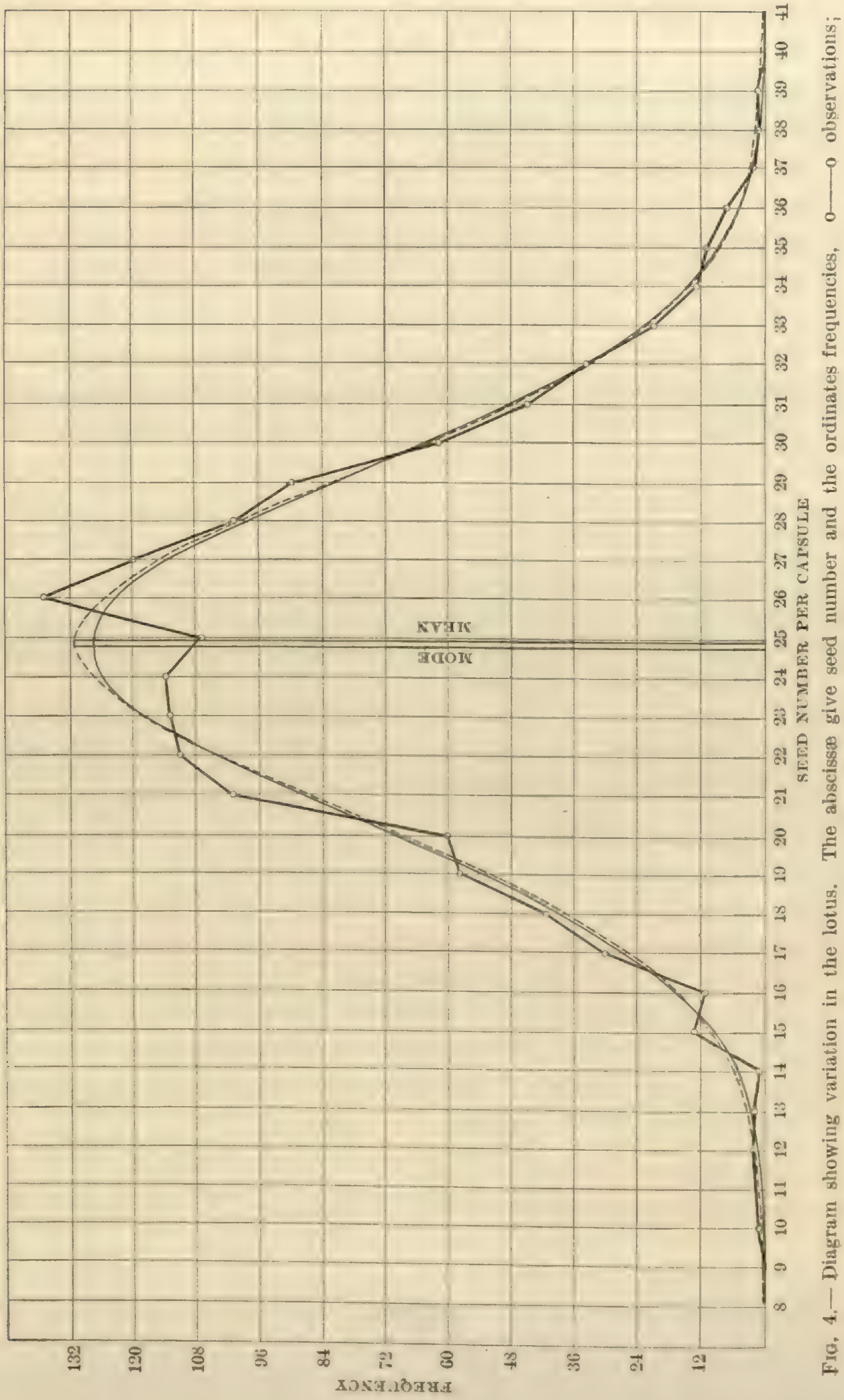

FIG. 4.— Diagram showing variation in the lotus. The abscissæ give seed number and the ordinates frequencies, o——o observations; ----, normal curve; ——, type 1 curve,

observation polygon in this region except as a result of random sampling.

The fact that this distribution approaches very closely to the normal type is indicated by the value obtained for the theoretical range of variation when a Type 1 curve is used. It will be recalled that this type of curve has the range limited in both directions, while the normal curve has an infinite range. Using the values of the moments given in Table 3, I find for the Type 1 curve:—

Total range = 60.8794
Lower limit of range = −3.9252
Upper " " " = 56.9541

It is clear that the theoretical range greatly overestimates the observed. Of course the start at −4 seeds appears at first sight to be an absurdity, but it must be remembered that this value is subject to a considerable probable error, and that it is possible to get as great an extension as this of the range of the theoretical curve below zero as a result merely of random sampling. Furthermore it must be admitted that while the upper limit of the range at 57 seeds seems very improbable, yet, for anything we know to the contrary, it is not impossible.[1] In general it is clear from this case that as the Type 1 curve approaches the normal its range becomes greatly extended.

There is one further point regarding this material to which attention should be called, namely, the bearing of the results on the question of the distribution of fecundity. It is evident that the number of seeds borne by a plant is the measure of its fecundity. In considering data like those here presented the question at once arises as to whether each different class of capsules contributes its proportionate share in the total number of seeds available for the propagation of a succeeding generation. A moment's consideration shows that this cannot be the case in Nelumbium. The figures given in Table 5 demonstrate this. To avoid the possibility of misunderstanding, the manner in which this table is formed may

[1] Since writing the above I have seen some actual statistics of variation in seed number in the lotus in which the upper limit of the observed range is 42 seeds, showing a tendency in the direction predicted by the theoretical curve.

be stated briefly. The figures in the second column were obtained by multiplying the number of seeds in a given capsule by the frequency with which that class of capsule occurred in the sample. The third column gives the same data reduced to *per mille* proportions.

TABLE 5

Total Number of Seeds borne by Capsules of Different Sizes

Capsule Class (Seeds per Capsule)	Total Number of Seeds borne in all Capsules of Designated Class	Per Mille Number of Seeds borne in all Capsules of Designated Class
9	9	0.26
10	0	0
11	0	0
12	24	0.68
13	26	0.74
14	14	0.40
15	195	5.56
16	176	5.02
17	510	14.54
18	738	21.04
19	1102	31.42
20	1200	34.21
21	2121	60.47
22	2442	69.63
23	2599	74.10
24	2736	78.02
25	2675	76.27
26	3562	101.56
27	3240	92.38
28	2828	80.63
29	2610	74.42
30	1860	53.03
31	1395	39.77
32	1088	31.02
33	693	19.76
34	442	12.60
35	385	10.98
36	252	7.19
37	74	2.11
38	38	1.08
39	39	1.11
Total	35,073	1000.00

From this table we see that, in round numbers, 1400 capsules produce 35,000 seeds. Further, it is clear that the different classes of capsules do not contribute in proportion to their frequency of occurrence to the total seed number. Thus, for example, a reference to Table 1 shows that capsules with 21 seeds each and capsules with 28 seeds each occur with equal frequency in our sample. But obviously the latter will contribute more to the total number of seeds. As a matter of fact the 28-seed capsules contribute 81 per thousand of the total number of seeds, as against 60 per thousand of the 21-seed capsules. Taking the data as a whole I find by a very simple calculation that:

(*a*) Capsules with *fewer* than the median number of seeds bear altogether 15066.325 seeds, or 42.96 percent of the total number.

(*b*) Capsules with *more* than the median number of seeds bear altogether 20006.675 seeds, or 57.04 percent of the total number. In other words 50 percent of the capsules produce 57 percent of the seeds, or, put in still another way, one half of the heads bears 14 percent more of the total number of seeds than does the other half. This result is, of course, an obviously necessary arithmetical consequence of the symmetry of the capsule distribution, yet it is a point which is frequently overlooked. A symmetrical distribution of the individuals of a population with respect to some measure of fecundity does not mean that the contributions of these individuals to the next generation even before selection will be represented by a symmetrical distribution. The very fact that the original distribution is symmetrical necessitates the contrary relation.

The results with reference to the proportionate contributions of the different classes of heads to the total seed number show the conditions before elimination begins. Many of the 35,000 seeds were undoubtedly incapable of germination, and after germination many more would be eliminated before reaching maturity. As to the distribution of the eliminating factors acting in the case of the lotus we know nothing. What I wish to emphasize here is that out of the total number of seeds before elimination begins, 57 percent are the product of one half of the parent heads and only 43 percent the product of the other half.

The results of this study may be summarized briefly as follows:

(1) In the variation in respect to number of seeds per capsule *Nelumbium luteum* follows very closely the normal or Gaussian law of the distribution of errors.

(2) Place constants are given for the designated character in the form unit of Nelumbium growing in Sandusky Bay.

(3) From the fact that the frequency distribution of the capsules in respect to seed number is symmetrical about the mean it follows that one half of the whole number of capsules bears 14 percent more of the total number of seeds available for a new generation than does the other half of the capsules.

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THE CAUSES OF EXTINCTION OF MAMMALIA

HENRY FAIRFIELD OSBORN

In studying the past history[1] of the Mammalia we find that in some cases the causes of the extinction are as obscure as in other cases they are obvious. I have thus been led to review the subject very carefully, gathering opinions and observations from various sources. I especially desire to arouse discussion and to receive criticisms and suggestions which will be warmly welcomed.[2]

History of Opinion

We find that while the main trend of present inquiry as to the external causes of extinction had been suggested by the middle of the nineteenth century, subsequent discoveries and observations furnish new and exact materials for induction both as to external and internal causes.

Cuvier, Lyell, Darwin.—The 'cataclysmal' views of Cuvier,[3] of wholesale destructions brought about by sudden and great geological changes, naturally gave way to the 'uniformitarian' views gradually developed from the time of Buffon to that of Darwin. The notions of the similarity of past and present causes, of the survival of the fittest, of internal causes of variation, development, and decline, gradually took their modern form. Whewell[4] clearly sets forth the opinions which developed between 1796 and

[1] Especially in connection with a monograph for the U. S. Geological Survey, entitled "The Titanotheres," which has been in preparation since 1900. This series of articles in the *Naturalist* will be embodied in somewhat modified form in the monograph.

[2] Address, Professor Henry Fairfield Osborn, American Museum of Natural History, New York.

[3] Cuvier, George. *Discours sur les révolutions de la surface du globe et sur les changements qu'ils ont produits dans le regne animal.* Paris, 1840. 1 vol. in 8vo.

[4] Whewell, —. *History of the Inductive Sciences*, vol. 3, 1837.

1837. Charles Lyell[1] gave the note for modern methods of research, greatly influenced Darwin, and perhaps exaggerated uniformitarianism.

In this very problem of extinction, however, uniformitarianism has a stout opponent in Henry H. Howarth. In his extremely interesting work *The Mammoth and the Flood* (London, 1878) he revives the theory of the destructive flood and marshals a vast number of facts to its support. "These facts," he observes (p. xvii), "I claim prove several conclusions. They prove that a very great catastrophe or cataclysm occurred at the close of the Mammoth period, by which that animal, with its companions, were [!] overwhelmed over a very large part of the Earth's surface. Secondly, that this catastrophe involved a very widespread flood of water, which not only killed the animals but also buried them under continuous beds of loam or gravel. Thirdly, that the same catastrophe was accompanied by a very great and sudden change of climate in Siberia, by which the animals which had previously lived in fairly temperate conditions were frozen in their flesh under ground and have remained frozen ever since."

The causes enumerated by Lyell in his later edition of the *Principles of Geology* after the publication of Darwin's *Voyage* and *Origin* are: (1) competition as affected chiefly by the introduction and extension of new forms, (2) agency of insects, *e. g.*, caterpillars, ants, locusts, in favoring or checking increase of plants and thus affecting the food supply of animals, (3) intimate reciprocal relations of animals and plants in the delicate balance of food supply, (4) disturbance of the equilibrium or balance of nature by the introduction of new insects, plants, vertebrated animals, (5) changes in physical geography affecting zoölogical and botanical provinces by new land or water connections, facilitating introduction of new competing forms, (6) causes especially potent in island life.

Referring to that subtle adjustment of the sum of all internal and external causes called the *balance of nature*, Lyell[2] observed:

"Every new condition in the state of the organic or inorganic

[1] Lyell, Charles. *Principles of Geology*, 1872.

[2] Lyell, Charles. *Principles of Geology*, vol. 2, New York, 1872, pp. 455–456.

creation, a new animal or plant, an additional snow-clad mountain, any permanent change, however slight in comparison to the whole, gives rise to a new order of things, and may make a material change in regard to some one or more species. Yet a swarm of locusts, or a frost of extreme intensity, or an epidemic disease, may pass away without any great apparent derangement; no species may be lost, and all may soon recover their former relative numbers, because the same scourges may have visited the region again and again, at preceding periods. Every plant that was incapable of resisting such a degree of cold, every animal which was exposed to be entirely cut off by an epidemic or by famine caused by the consumption of vegetation by the locusts, may have perished already, so that the subsequent recurrence of similar catastrophes is attended only by a temporary change."

Even as a geologist Lyell was very cautious, certainly too cautious, in estimating the destructive influence of geologic and physiographic changes. In 1863 (*Antiquity of Man*,[1] p. 374), he observed:

"It is probable that causes more general and powerful than the agency of Man, alterations in climate, variations in the range of many species of animals, vertebrate and invertebrate, and of plants, geographical changes in the height, depth, and extent of land and sea, some or all of these combined, have given rise, in a vast series of years, to the annihilation, not only of many large mammalia, but to the disappearance of the *Cyrena fluminalis*, once common in the rivers of Europe, and to the different range or relative abundance of other shells which we find in the European drifts."

Charles Darwin[2] pursues a line of thought exactly prophetic to that of Lyell in discussing the Pliocene and post-Pliocene extinction of the large mammals of South America. He dismisses any catastrophic causes and in general attributes extinction to a *cessation of those world-wide conditions of life which were favorable to the larger quadrupeds* in Europe, Asia, Australia, North and

[1] Lyell, Charles. *Geological Evidences of the Antiquity of Man*, 2d ed., revised, 8vo, London, 1863, p. 374.

[2] Darwin, Charles. *Journal of Researches....Voyage of H. M. S. Beagle*, 8vo, 1834, pp. 169, 170.

South America. In South America and elsewhere (1) he does not favor the extreme theory of the destructive influence of the Glacial Epoch and he cites the supposed post-Glacial survival of Macrauchenia and Mastodon. "It could hardly have been a change of temperature," he observes (p. 170), "which at about the same time destroyed the inhabitants of tropical, temperate, and arctic latitudes on both sides of the globe." (2) He dismisses the possibility of extinction by man. (3) Also of an extended drought in South America, calling attention to the Pampean horse as an animal which could have survived a drought.

In seeking to establish a general law of extinction Darwin makes the following propositions: (1) the natural increase of animals is in geometrical ratio, while, (2) the food supply remains constant, thus (3) any great increase in numbers is impossible and must be checked by some means. (4) We are seldom able to state the cause of this check beyond saying that it is determined by some slight difference in climate, food, or the number of enemies. (5) We are, therefore, driven to the conclusion that causes generally quite inappreciable by us determine whether a given species shall be abundant or scanty in numbers. (6) Comparative rarity is the plainest evidence of less favorable conditions of existence. (7) Rarity frequently precedes extinction, and if the too rapid increase of species, even the most favored, is steadily checked, why should we feel such great astonishment at the rarity being carried a step farther to extinction.

These were Darwin's earlier views expressed in *The Voyage*. In *The Origin of Species* he discusses fully the checks to increase as follows: (1) climate as directly unfavorable, (2) as indirectly unfavorable by favoring other forms or by increasing the number of certain competitors. (3) Unchecked increase frequently followed by epidemics — possibly in part by facility of diffusion of parasites amongst the crowded animals. (4) Finally, since a large stock of individuals, relatively to the number of enemies, is absolutely necessary for the preservation of a species a diminished number would tend to extinction. (5) Any form (p. 133) which is represented by few individuals will run a good chance of utter extinction, during great fluctuations in the nature of the seasons, or from a temporary increase in the number of its enemies. (6) Diminution

in number presents less opportunity for producing favorable variations — hence rare species will be less quickly modified or improved within any given period.

Alfred Russell Wallace observes: "To discover how the extinct species have from time to time been replaced by new ones down to the very latest geological period, is the most difficult, and at the same time the most interesting problem in the natural history of the earth."[1] Also: "Whenever the physical or organic conditions change to however small an extent, some corresponding change will be produced in the flora and fauna, since, considering the severe struggle for existence and the complex relations of the various organisms, it is hardly possible that the change should not be beneficial to some species and hurtful to others."[2]

The majority of these speculations of these great naturalists have been abundantly confirmed. The opinions of many subsequent writers on this subject may be stated under their proper headings.

External Causes of Extinction

Physical Environment. Geological and Physiographic Changes

We may first consider those causes of extinction which originate with changes in the environment.

Changes of Land Masses and their Connections

Changes of land masses caused by elevation or subsidence operate indirectly through causing changes in all the physical conditions of climate, moisture, or dessication, temperature, etc.; also more directly in facilitating or cutting off migrations, in introducing new competition, etc.

Diminished or Contracted Land Areas.— The stable continents, North America and Africa, underwent slight fluctuations of land area in Tertiary times as compared with the highly unstable continents of Europe, of Australia, and of the southern half of South

[1] Wallace, Alfred R. *Natural Selection*, p. 14.
[2] Wallace, Alfred R. *Darwinism*, 1889, p. 115.

America. In Europe the varying coast lines, the insular conditions, the archipelagic surfaces are to be more seriously studied than they have been in connection with extinction, although it must be stated at once that the main phenomena of extinction in unstable Europe coincide with those in stable America.

Wallace discussed the extinction of the large Pliocene Australian mammals chiefly from this standpoint (see also p. 785). He (*Geog. Dist. Mam.*, 1876, vol. 1, pp. 158-159) attributed the Australian extinction chiefly to the possible glacial conditions and to the increased competition and struggle for existence caused by the progressively contracted land area due to subsidence.

The substitution of *insular* for *continental* conditions by subsidence has undoubtedly been a potent cause both of extermination in certain localities and of the survival of very primitive forms (Wallace), *e. g.*, Monotremata and Marsupialia in Australia. While the *contraction of land areas* may have resulted in general extinction, this has not yet been demonstrated.

Insular Conditions.— On islands we observe local dwarfing and extinction rather than the general extinction of a family or order which is our real subject. Of island life, so thoroughly studied by Wallace, it may be said at once that most of the causes both of survival and extinction which prevail on continents are *intensified on islands.* Wallace rightly attributes the survival of the Monotremata and Marsupialia to the practically insular condition of the Australian region. Lyell, Wallace, and others cite many instances of profound and rapid modifications caused by the introduction of new forms on islands.

PHYSICAL ENVIRONMENT. CHANGES OF CLIMATE

We have to consider temperature and moisture as brought about by geologic and physiographic changes, and also as affected by biotic changes or changes in the fauna and flora.

Increasing Cold

Influence of Secular Cold.— The effects of secular lowering of temperature must be analyzed with some care. At first sight

the theory of extinction through the direct action of cold is very simple, but it is found that some cases of extinction during the Glacial Period, of the horse in North America for example, do not admit of this explanation. It is more in accord with the facts to say that the Glacial Period originated certain new conditions of life which hastened extinction; these conditions relate to enforced migration, to overcrowding, to feeding, reproduction, mating, relations to enemies, deforestation, and other indirect results.

Protective Adaptation to Secular Cold.—Resistance to cold depends upon (*a*) internal heat-producing power which is a progressive adaptation of the higher Mammalia, (*b*) the acquisition of a warm external covering. The well known cases of adaptation to extreme cold among the elephants (*E. primigenius*, woolly mammoth), rhinoceroses (*R. tichorhinus*, woolly rhinoceros), horses (*E. przewalskii*), and certain northern ruminants, such as the camels and musk oxen, show that we must not assume that cold was in all cases the sole or direct cause of extinction.

Glacial and Post-Glacial Extinction.—Wallace observes: "....We have proof in both Europe and North America, that just about the time these large animals were disappearing, all the northern parts of these continents were wrapped in a mantle of ice; and we have every reason to believe that the presence of this large quantity of ice (known to have been thousands of feet if not some miles in thickness) must have acted in various ways to have produced alterations of level of the ocean as well as vast local floods, which would have combined with the excessive cold to destroy animal life."[1] And again: "....We can therefore hardly fail to be right in attributing the wonderful changes in animal and vegetable life that have occurred in Europe and North America between the Miocene period and the present day, in part at least, to the two or more cold epochs that have probably intervened. These changes consist, first, in the extinction of a whole host of the higher animal forms; and, secondly, in a complete change of types due to extinction and emigration, leading to a much greater difference between the vegetable and animal forms of the Eastern and Western hemispheres than before existed."[2]

[1] *Geographical Distribution of Animals*, vol. 2, p. 151.
[2] Wallace, A. R. *Island Life*, 1881, p. 117.

Certainly the most direct instance of a great extinction of quadrupeds contemporaneous with a secular change of climate is that of the Glacial Period in the entire northern hemisphere. The close of the Pliocene or beginning of the Pleistocene found North America peopled with the following kinds of great quadrupeds, all of which disappeared during the Ice Age.

Artiodactyla	Camelidæ	Camels
		Llamas
Perissodactyla	Equidæ	Horses
	Tapiridæ	Tapirs
Proboscidea	Mastodontinæ	Mastodons
	Elephantinæ	Elephants
Edentata	Gravigrada	Giant Sloths
		Megalonyx
		Megatherium
		Paramylodon
	Glyptodontia	Glyptotherium

Numerical Diminution of Camelidæ.—The Glacial Period was heralded by increasingly severe winters and cold waves. The observations of Prichard in Patagonia throw a light on the numerical diminution of the Camelidæ.

"Around the lake lay piled the skulls and bones of dead game, guanaco (*Lama huanachus*) and a few huemules (*Furcifer chilensis*). These animals come down to live on the lower ground and near unfrozen water during the cold season, and there, when the weather is particularly severe, they die in crowds. We saw their skeletons, in one or two places literally heaped one upon the other" (*Through the Heart of Patagonia*, 1902, p. 132). "Again we came upon a second death-place of guanaco, which made a scene strange and striking enough. There cannot have been less than five hundred lying there in positions forced and ungainly as the most ill-taken snapshot photograph could produce. Their long necks were outstretched, the rime of the weather upon their decaying hides, and their bone-joints glistening through the wounds made by the beaks of carrion-birds. They had died during the severities of the previous winter, and lay literally piled one upon another" (*op. cit.*, p. 189). "The meaning of this I gathered from Mr. Ernest Cattle. He told me that in the winter of 1899 enor-

mous numbers of guanaco sought Lake Argentino, and died of starvation upon its shores. In the severities of winter they seek drinking-places, where there are large masses of water likely to be unfrozen. The few last winters in Patagonia have been so severe as to work great havoc among the herds of guanaco" (*op. cit.*, p. 255).

Deforestation and Secular Cold.—After considering the conditions in Alaska, Mr. A. G. Maddren[1] summarizes his conclusions as follows: "I. That while remnants of the large Pleistocene mammal herds may have survived down to the Recent period and in some cases their direct descendants, as the musk-ox, to the present, most of them became extinct in Alaska with the close of the Pleistocene.

"II. The most rational way of explaining this extinction of animal life is by a gradual changing of the climate from more temperate conditions permitting of a forest vegetation much farther north than now, to the more severe climate of today, which subduing the vegetation and thus reducing the food supply besides directly discomforting the animals themselves, has left only those forms capable of adapting themselves to the Recent conditions surviving in these regions to the present."

Influence of Cold and Snow on Food Supply and Choice of Food.—The deaths of great numbers of animals from hunger or starvation through the covering of food during the winter season under heavy layers of snow are commonly observed among the large herds of some of the domesticated horses and cattle on the Western plains. In fact, it is most probable that during the glacial period the great winter snow blankets covering the natural food rather than the actual influence of the cold itself, was the chief cause of extinction.

Under these conditions horses are driven to food, such as the branches of willows, which is very deleterious to them. Under the influence of hunger cattle and sheep also will feed eagerly and indiscriminately on plants which may be injurious to them or to their young, as recorded by Chestnut and others in the United

[1] Maddren, A. G. "Smithsonian Exploration in Alaska in 1904, in Search of Mammoth and other Fossil Remains." *Smiths. Misc. Coll.*, vol. 49, p. 65.

States Agricultural Department. The indirect results of hunger may be, therefore, quite as effective as actual starvation.

Animals vary greatly in adaptability to new conditions caused by prolonged cold and heavy snowfall. Horses remove snow even to depths of three or four feet and find food to carry them through the winter, while cattle under the same conditions starve.

An interesting instance of the effects of a temporary lowering of temperature in a subtropical region is that cited by Bangs of the influence of an unusual cold wave in the habitat of one of the Sirenia (*Manatus manatus*) in the rivers of Florida in the winter of 1895. The author observed that an unusual cold wave cut down all the leaves of the mangrove, a favorite food of the manatee at certain seasons. This was followed by a marked numerical diminution of the manatee.[1]

Dangers of Numerical Diminution and Diminished Herds.— While distinction must be drawn between actual extinction and a *temporary diminution* in numbers caused, for example, by cold waves, prolonged or repeated droughts, floods, epidemics, and other unfavorable conditions of life, it is very important to observe, as suggested by Darwin, that diminution in numbers may lead to extinction in certain cases. For example, a herd of animals may be reduced to the danger point in numbers where they can no longer protect their young. Director Bell of the Canadian Geological Survey believes that the small herd of Woodland Bison of British Columbia, now thoroughly protected by the government, will be destroyed gradually through the killing of the calves by wolves, the bulls not being sufficiently numerous to protect the calves.

Diminished Herds and Inbreeding.— Diminished herds in restricted regions may also disappear through too close inbreeding. On this familiar subject see Gerrit S. Miller's[2] paper "Fate of the European Bison Herd," in which the author shows the possibly fatal influence of inbreeding on diminished herds, although it must be pointed out that the animals are protected and are thus *living under unnatural conditions.*

[1] Mr. C. H. Townsend, from observations in the New York Aquarium, is inclined to attribute this diminution to the respiration of the frosty air.

[2] Miller, Gerrit S., Jr. "The Fate of the European Bison Herd." *Science*, n. s., vol. 4, no. 99, Nov. 20, 1896, pp. 744–745.

In a paper entitled "Das allmähliche Aussterben des Wisents (*Bison bonasus* Linn.) im Forste von Bjelowjesha",[1] Mr. Eugen Büchner gives a detailed history of the bison herd in the Bieloviejsha (or Bialowitza) forest, Province of Grodno, in Lithuania, Russia, during the present century. "A careful study of the breeding habits of the bison in the Bieloviejsha forest and elsewhere leaves no room for doubt that the present slow rate of reproduction is an abnormal condition, and that to it is due the rapid approach of the extinction which is the certain fate of the herd under consideration. This diminished fertility the author regards as a stigma of degeneration caused by in-breeding.... Another indication of the degenerate condition of the Bieloviejsha herd is seen in the great excess of bulls, which probably outnumber the cows two to one. This is doubtless a result of in-breeding, for Düsing (*Jen. Zeits. f. Naturw.*, Bd. xvii, p. 827, 1884) has shown that close in-breeding, like a reduced condition of nutrition, is favorable to the production of an excess of males.... In conclusion, the author considers that his studies of the history of the Bieloviejsha bison leave scarcely room for doubt that in-breeding is the cause of the final extinction of most large mammals. In-breeding must begin and lead gradually but certainly to the extinction of a species when it, through any cause, has become so reduced in numbers as to be separated into isolated colonies."

Influence of Cold during the Reproduction Period.— Exceptional cold waves or unusually prolonged cold seasons may cause a temporary loss of food supply or cause the death of the young, which in northern latitudes are usually born in spring. The diminution or loss of young from this cause might act as the first of a series of destructive effects of a progressive secular change. These may be summarized as follows from actual zoölogical observations[2] among the Cervidæ: (*a*) disturbed conditions during the conjugation (pairing, mating, rutting) period; (*b*) enfeebled (through hunger) condition of females during parturition period; (*c*) severe weather conditions, ice-storms, crusted snow, prolonged

[1] Büchner, Eugen. *Mém. Acad. Impér. des Sci. de St. Pétersbourg*, vol. 3, no. 2, 1895, p. 1–30.

[2] Communicated by Mr. Madison Grant, Secretary of the Zoölogical Society of New York.

wet and sleet at time of birth; (*d*) bulls unable to protect herds; (*e*) cows unable to protect young from Carnivora through starved condition, or abandoning them when attacked by wolves; (*f*) enfeebled and unprotected condition of quadrupeds favorable to increased food supply and consequent multiplication of cursorial and other Carnivora, especially Canidæ and Felidæ.

These zoölogical observations are to a certain extent borne out in paleontology by Leith Adams' (*British Fossil Elephants*, 1879, part 2, p. 98) observations of the exceptionally large number of milk teeth of elephants found in certain Pleistocene deposits, which appears to indicate a high mortality of the young.

Temperature Control of Fertility and Reproduction.— Merriam[1] has directed attention to one of the physiological effects of a lowering of temperature, namely, its influence upon diminished or increased fertility and the rate of reproduction in what he has called the 'law of temperature control'. This he has stated as follows: temperature by controlling reproduction predetermines the possibilities of distribution; it fixes the limits beyond which species cannot pass; it defines broad transcontinental barriers within which certain forms may thrive if other conditions permit, but outside of which they cannot exist, be the other conditions never so favorable, (because the sexes are not fertile).

(1) *Temperature.* In discussing how species are checked in their efforts to overrun the earth Merriam points out that more important than geographic barriers are the *climatic barriers* (as observed by Humboldt), and of these that temperature is more important than humidity. First, in 1892, this author attempted to show (*Proc. Biol. Soc. Washington*, vol. 7, April, 1892, pp. 45, 46) that the distribution of terrestrial animals is governed less by the yearly isotherm or mean annual temperature than by the total rather than the mean temperature during the period of reproductive activity and of growth (adolescence). This reproductive period in the tropics extends over many months or nearly the whole year, and within the Arctic Circle and summits of high mountains is of two months or less duration. Later, in 1894, results which

[1] Merriam, C. Hart. "Laws of Temperature Control of the Geographic Distribution of Terrestrial Animals and Plants." *Nat. Geogr. Mag.*, vol. 6, Dec. 29, 1894.

Merriam obtained from extensive comparison of temperatures and distribution justified the belief that animals and plants (Lower Austral and tropical types coming from the South) are restricted in northward distribution by the total quantity of heat during the season of development and reproduction. Conversely animals and plants (Upper Austral, Transition, and Boreal types coming from the North) are restricted in southward distribution by the mean temperature of a brief period covering the hottest part of the year. Thus in the Transition Zone, Boreal and Austral types mingle in the equable climate of the Pacific coast of California while they are sharply separated by the inequable extremes of cold and heat of the interior continental plateau.

(2) *Humidity*, observes Merriam, is a less potent factor than temperature in limiting the distribution of the Mammalia of North America.[1] (*a*) Many genera adapted to certain restrictions of temperature zones range east and west completely across the American continent inhabiting alike the humid and arid subdivisions but no genus adapted to certain restrictions of humidity ranges north and south across the temperature zones. (*b*) Thus humidity governs the details of distribution of a few species of mammals within the temperature zones.

Lowering of Temperature and Diminished Fertility as a Cause of Extinction.—Since the favorable influence of high mean temperature on fertility and reproduction is well illustrated in the reproductive organs of birds and in the early age of reproduction and increased fertility of the human species toward the equator, and since there exist these low-temperature barriers to reproduction, it is highly probable that a secular lowering of temperature may have repeatedly been a cause of extinction in the earth's history; that certain mammals may have resisted exposure to cold or discovered new forms of food and yet suffered extinction through the subtle inhibition of fertility and reproduction.

Increasing Moisture

Influences of Increased Rain Supply.—Besides the changes in

[1] This would not be true of Africa, of Central America, or other tropical countries where certain insect and disease barriers exist which are favored by moisture.

plant food which are brought about by diminished moisture, as indicated below, there are the effects of increased moisture which may be equally if not more important. Dry or moderately dry conditions, provided they are not too extreme, are generally more favorable to quadrupeds than moist conditions. The plains and forest regions most densely populated with quadruped life, such as those of the African plateau, are regions of moderate rainfall and even of prolonged summer droughts. The regions least densely populated are regions of heavy rainfall and most dense forests and vegetation, such as those of the equatorial belt of South America or the Congo region of Africa. We observe that:

(1) Increased rainfall may diminish the supply of harder grasses to which certain quadrupeds have become thoroughly adapted.

(2) Increased rainfall may introduce new poisonous or deleterious plants (see p. 790).

(3) It may be the means of introducing new insect and other pests and new insect barriers.

(4) It may be the means of introducing new protozoan diseases, and new insect carriers of diseases.

(5) It may be the means of erecting new forest barriers or new forest migration tracts for certain Carnivora. It follows that periods of secular increasing moisture such as the early Pleistocene of the northern hemisphere is supposed to have been, may have been very unfavorable to certain large quadrupeds, even prior to the advent of extreme cold.

Insect Barriers and Moisture.—It is a matter of universal observation that in tick- or insect-infested countries, generally, dry seasons result in the reduction, moist seasons in the increase of diseases. Dry localities are favorable; moist localities are unfavorable.

Thus A. E. Shipley observes of the tse-tse fly, in his interesting address[1] that its "northern limit corresponds with a line drawn from the Gambia, its southern limit is about on a level with the northern limit of Zululand. Most writers agree that the tse-tse is not found in the open veldt, that it must have cover. Warm, moist, steamy hollows, containing water and clothed with forest growth are the haunts chosen."[1]

[1] Shipley, Arthur E. "Insects as Carriers of Disease." *Nature*, vol. 73, no. 1888, Jan. 4, 1906, pp. 235–238.

Decreasing Moisture. Secular Desiccation

Secular desiccation has been the fate of portions of three great continents, and on each continent we observe a general concomitant modification and extinction of certain kinds of quadrupeds. The great regions of the world where decreasing moisture has introduced a series of changes ending in the extinction of a great number of quadrupeds are:

(1) North America, Western Plains Region, Arid Plateau and Mountain Region beginning in Oligocene times.

(2) South America, Patagonia and Pampean Region, beginning in late Pliocene times.

(3) North Central Africa, the Fayûm district beginning in Oligocene times.

(4) Central Australia, beginning in Pleistocene times.

The writings of American paleontologists, also of Stirling, of Andrews, and of Ameghino, describe faunæ adapted to much moister conditions than those which prevail at present. We observe that decreasing moisture:

(1) Changes the character of the food supply. Diminution of softer and more succulent vegetation, increase of harder and more resistant vegetation.

(2) Increases length and severity of the dry season.

(3) Removes forest barriers and admits new competitors.

(4) Reduces the water supply and eliminates animals incapable of traveling long distances for food and water.

(5) Favors grazing quadrupeds and eliminates browsing and forest-living quadrupeds.

Prolonged or increasing droughts entirely disturb the balance of nature; they compel migrations; they expose quadrupeds to Carnivora by driving them to restricted water pools. They favor quadrupeds able to dispense with a daily supply of water.

Secular Desiccation and Vegetation.—The indirect influences of secular changes of climate on quadrupeds are apparently quite as important factors in extinction as the direct, namely, changes in vegetation due to diminution of moisture, which render certain types of quadrupeds which were perfectly adapted to one kind of

plant food, largely or wholly inadapted to the new or altered kinds of food. This we shall show was probably the most potent factor in the extinction of the Titanotheres, of the Chalicotheres, in fact of all the quadrupeds with short-crowned molar teeth, adapted to browsing habits.

The correlation between an initial change of climate and the consequent diminution of the softer kinds of vegetable food and increase of the harder kinds, such as grasses, followed by the extinction of a very large number of Herbivora, was first thoroughly worked out in an epoch-making memoir of Waldemar Kowalevsky in 1873.

Droughts and Numerical Diminution.— Darwin[1] describes the devastating effects of the great drought in the Pampas between 1827 and 1830 in which great numbers of birds, wild animals, cattle, and horses, perished from want of food and water. The cattle perished by thousands on the muddy banks of the Parana River. Similarly Azara describes the horses perishing in large numbers in the marshes.

Increasingly prolonged summer droughts were characteristic of the late Miocene and Pliocene of Europe, and we are beginning to accumulate evidence that the same conditions prevailed in North America.

Influence of Droughts in Central Africa.— The influence of the gradual decrease of moisture in a country is clearly illustrated in the conditions which prevail in the African continent to-day, as observed by such writers as Gregory,[2] Foa, and Schillings. Thirst, like hunger, first drives quadrupeds to take extreme risks, which they would absolutely avoid during natural conditions. The drinking-places or water-pools during long seasons of drought become fewer in number and more widely separated, and large animals driven to them by thirst are more readily attacked and killed by Carnivora. The pools become separated by distances of thirty and forty miles, thus necessitating long excursions to and from the various feeding places, in which the quadrupeds are

[1] Darwin, Chas. *Journal....Voyage of H. M. S. Beagle around the World*, p. 128–130.

[2] Gregory. *The Great Rift Valley*....8vo. London, 1896.

again exposed to attack. Finally some of the pools dry up entirely and, as observed by Gregory, (p. 268): "Here and there around a water hole we found acres of ground white with the bones of rhinoceroses and zebra, gazelle and antelope, jackal and hyena ....all the bones were there fresh and ungnawed...." These animals, which had not migrated, had "crowded around the dwindling pools and fought for the last drops of water."

Such perishing of animals in great numbers from thirst would bring about the condition of *diminished herds* spoken of above as the final cause of extinction through inability to protect the young.

Alkali and Salt Deposits.— One effect of increasing desiccation is the increased number of alkali lakes, licks, and springs, and other localities of salt deposits. Alkali is much sought by certain wild animals as a substitute for salt. Western stock-raisers disagree as to the effects of alkali upon sheep and cattle, some believing that it cannot take the place of salt. Chestnut (1901, p. 20) notes that alkali may possibly predispose to the 'loco habit,' the eating of a narcotic weed (see p. 791). When domesticated animals are not salted regularly they soon discover localities where large quantities of alkali are found in the soil and visit such places frequently for the purpose of eating this alkali soil (Chestnut, 1901, p. 87).[1]

Desiccation and Extinction in Central Australia.— Wallace's opinion as to Australian extinction has been cited more with reference to the effect of Glacial-Epoch conditions and continental contraction in general than as to the special causes of extinction in Australia.

More recent research as set forth by the geologist Professor Tate,[2] the zoölogists Hedley[3] and Baldwin Spencer, show that in Pliocene times heavy rainfall or pluvial conditions, great inland

[1] Chestnut, V. K., and Wilcox, E. V. "The Stock-poisoning Plants of Montana: A Preliminary Report." *U. S. Dept. of Agric., Div. of Botany,* bull. 26, 1901.

[2] "On the Influence of Physiographic Changes in the Distribution of Life in Australia." *Austr. Ass. Adv. Sci.*, vol. 1, pp. 312–325, 1889. Quoted by Baldwin Spencer. *Through Larapinta Land; A Narrative of the Horn Expedition to Central Australia,* Part 1, p. 159, 1896.

[2] "The Faunal Regions of Australia." *Austr. Ass. Adv. Sci. Adelaide,* 1893.

seas or freshwater lakes (first surmised by Stuart) favored the development of large marsupials. Conversely the rise of an eastern coastal range was followed by diminished rain supply and progressive desiccation of the interior region.

Spencer observes:[1] "The larger forms now extinct, such as species of Diprotodon, Nototherium, Phascolonus, Macropus, Protemnodon, etc., reached their greatest development in Pliocene times and were characteristic of the eastern interior, spreading southward round the western end of the Dividing Range into Victoria. They do not seem to have reached the eastern coastal district. . . . . In Post-Pliocene times, with the increasing desiccation of the whole central area they became extinct, though this extinction cannot be attributed wholly to the drying up of the land, because in certain parts, such as Western Victoria, to which they reached, the state of desiccation did not supervene; but at the same time it may perhaps be justly argued that the desiccation of the vast area of the interior was the largest factor in their extinction."

The discovery (1892) of the great Lake Callabonna bone deposit in the interior of South Australia abundantly confirms the 'desiccation' theory. Dr. E. C. Stirling[2] describes this remarkable deposit as follows: —

"There is, however, compensation for the unpromising physical features of Lake Callabonna in the fact that its bed proves to be a veritable necropolis of gigantic extinct marsupials and birds which have apparently died where they lie, literally, in hundreds. The facts that the bones of individuals are often unbroken, close together and, frequently, in their proper relative positions (*vide* pl. A, fig. 3), the attitude of many of the bodies and the character of the matrix in which they are embedded, negative any theory that they have been carried thither by floods. The probability is, rather, that they met their death by being entombed in the effort to reach food or water, just as even now happens in dry

[1] Spencer, Baldwin. *Report of the Horn Expedition to Central Australia. Summary of the Zoological, Botanical and Geological Results of the Expedition*, 1896, p. 183.

[2] Stirling, E. C. "Fossil Remains of Lake Callabonna." *Mem. Roy. Soc. of South Australia*, vol. 1, pt. 2, pp. ii–iii.

seasons, to hundreds of cattle which, exhausted by thirst and starvation, are unable to extricate themselves from the boggy places that they have entered in pursuit either of water or of the little green herbage due to its presence. The accumulation of so many bodies in one locality points to the fact of their assemblage around one of the last remaining oases in the region of desiccation which succeeded an antecedent condition of plenteous rains and abundant waters. An identical explanation has been suggested by Mr. Daintree[1] in his 'Notes on the Geology of the Colony of Queensland.'"

Living Environment. Plant Life

Under climate we have considered the relations of cold, heat, moisture, and desiccation to hunger, thirst, the feeding and migrating habits of animals. We may now look at the food supply of the Herbivora in relation only to *unusual conditions of life*.

Forestation, Deforestation, and Reforestation.—Forests furnish the necessary conditions of life of certain quadrupeds, especially of the browsers and of the Proboscidia. Among Artiodactyla the deer, among Perissodactyla the tapirs are typical forest animals. Conditions, therefore, which cause deforestation would become a means of extinction; such conditions are (*a*) intense cold and heavy snow capping, (*b*) intense dryness, (*c*) destruction of young trees by the smaller browsing animals. It is probable that the interior of Australia and the Pampean region of South America were in Pliocene and early Pleistocene times partially covered with forests. It is certain that the Holarctic region or circumpolar belt was forested in the early Pleistocene. Our western arid region was extensively forested at one period. Several of the smaller islands of the Mediterranean have been deforested. Reforestation would confine and limit the desert and plains types. Progressive moisture and reforestation would be very unfavorable to the horse (see Morris, 1895, p. 261). Thus both migration barriers and migration tracts are formed by forests.

[1] *Quart. Journ. Geol. Soc.*, vol. 28, 1872, p. 275.

A New or Altered Food Supply

Poisonous Plants.—Plants which are fatal to some Herbivora are innocuous to others. Linnæus in his *Tour in Scania* tells us, as cited by Lyell [1] "that goats were turned into an island which abounded with the *Agrostis arundinacea*, where they perished by famine; but horses which followed them grew fat on the same plant. The goat, also, he says, thrives on the meadow-sweet and water-hemlock, plants which are injurious to cattle." [2]

We must be extremely cautious not to substitute artificial conditions or those brought about by the agency of man for purely natural conditions. In speaking of the deaths caused by the twenty-five species of stock-poisoning plants found in Montana, Chestnut [3] observes: "But all these causes operate much less effectively against buffaloes and other ruminants in the wild state for, in the first place, being bred there under perfectly natural conditions, and being abundantly able to roam over long distances in search for food and water, they naturally reject all but the best and most wholesome diet. Then in the winter they migrate to the south, where the conditions for their existence were more favorable....Besides, it would require a large quantity of any of the common poisonous plants to kill an animal of such size."

Observations in South Africa [4] give similar results. The 'chinkerinchee' plant (Ornithogalum) is poisonous to horses, and one of the ragworts (Senecio) is an irritant causing cirrhosis of the liver in cattle and horses. Other plants which give trouble are tulps (species of Moræa). The losses are chiefly among cattle not accustomed to the country, or amongst very hungry trek cattle.

It is true, first, that animals generally but not invariably learn to avoid poisonous plants, second, that they become more or less immune to their deleterious effects, third, that often it is solely

[1] *Principles of Geology*, vol. 2, p. 440, 1872.

[2] *Ibid.*, vol. 7, p. 409.

[3] "Some Poisonous Plants of the Northern Stock Ranges." *Yearbook Dept. Agriculture for 1900, Washington*, pp. 308–309.

[4] Kindly communicated by Charles P. Lounsbury, of the Department of Agriculture, Cape of Good Hope. See *Agricultural Journal*, February, 1906.

the influence of hunger which drives them to eat poisonous plants. This justifies the consideration of plants under unusual conditions of life among the possible causes of extinction. The presence of molds and smuts which appear on the Gramineæ, the introduction and spread of certain narcotic plants, the influence of ergot in causing diseases of the hoof, the relation of poisonous plants to increased or diminished rainfall, the introduction of certain poisonous plants which while not injuring the parent affect and frequently kill the suckling young may be considered. Lambs are frequently killed by sucking milk from animals which had fed on the death camas, *Zygadenus venenosus*.[1]

Dangers Heightened by Harsh or Unusual Conditions of Life

Poisonous plants are widely distributed. Under the unnatural conditions of extreme cold, drought, enforced migration, starvation, etc., it is not impossible that they may have exerted some influence especially on *diminishing herds*. The following observations are chiefly brought together from the papers of Dr. V. K. Chestnut of the U. S. Agricultural Bureau. This author states in a letter dated July 9, 1902: "So far as my observations have extended the chief circumstance leading to death from poisonous plants is an irregularity of the food supply caused by more or less unusual conditions. It does not seem reasonable to suppose that wild animals are frequently poisoned in their native grazing grounds. Sudden disasters, however, might drive them from their feeding grounds into pastures quite unfamiliar to them, where they would undoubtedly be more or less at a loss to distinguish between poisonous and non-poisonous plants."

The following observations (*a*, *b*, *c*) apply to domesticated Herbivora.

(*a*) *Varying Effects of Wet and Dry Months.*—Chestnut ("Stock-Poisoning Plants of Montana" 1901, p. 19) observes that the majority of plants known to be especially poisonous during the wet months are so shriveled and dry in the dry months as to be

[1] Chestnut, V. K., and Wilcox, E. V. *Stock Poisoning Plants of Montana.* p. 61.

absolutely unpalatable. Sheep owners have accordingly found mountain ranges which are extremely dangerous for sheep during the wet months of early summer, quite safe during the months from July to September inclusive. Similarly, during the wet season and when feeding immediately after heavy rainstorms domesticated animals are more apt to pull up the roots of plants than when the ground is dry (Chestnut, 1901, p. 26), and, as is well known, in the case of many poisonous plants it is the roots which chiefly contain the active principle.

(*b*) *Fatal Effects of Snowstorms.*—After heavy snowstorms when the grass is covered by snow it often happens that only the taller species of plants are exposed (Chestnut, 1901, p. 27). In such cases the poisonous larkspurs (*Delphinium glaucum*) are greedily eaten by cattle, which would otherwise avoid these plants. This tendency is increased by the fact that ruminants do not feel at ease so long as the stomach is not full and are inclined to eat anything in sight after a snowfall. In seasons of drought certain poisonous leguminous plants remain green and tempting after the grasses have become thoroughly dried. Under these conditions cattle on the range are known to take the loco and lupin (Chestnut, 1901, p. 29).

(*c*) *Fatal Effects of Enforced Migration.*—It is observed (Chestnut, 1901, p. 21) among domesticated animals that when feeding quietly on the range they exercise considerable choice in the selection of forage plants, but when being driven six or eight miles a day they are frequently forced by hunger to bite off almost all kinds of plants which grow along their course. Enforced migration among wild animals might similarly cause them to become less fastidious about food.

Dangerous Plants Favored by Moisture

Poisonous Plants of Montana.—The chief poisonous plants of the Montana stock ranges (Chestnut, 1901) are: the death camas (Zygadenus), favored by moderate moisture and taken by sheep; the "tall larkspur" (*Delphinium glaucum*), favored by moderate moisture, taken by cattle; the "purple larkspur" (*D. bicolor*), taken by sheep; the water hemlock (Cicuta), found along water

courses, taken by cattle and sheep; the white loco (Aragallus), taken by horses, sheep, and cattle. Lupines (Lupinus) in certain stages of growth are poisonous to sheep. Ergot (*Claviceps purpurea*), occurs in Montana on a variety of grasses, and is occasionally poisonous to horses and cattle, producing a disease of the limbs. On a large ranch of Wyoming, ergot is reported (Walter Granger, letter, 1904) to have appeared as *a result of irrigation* rendering a large tract fatal to horses and cattle by causing a disease of the hoofs.

A leguminous plant of Egypt, *Lotus arabicus*, recently investigated by Dunstan and Henry,[1] as a growing plant, is quite poisonous to horses, sheep, and goats. Its seeds when ripe are commonly used as fodder. It contains a glucecoid termed 'lotusin,' which is poisonous when taken into the stomach (Chestnut, 1902).

Narcotic Plants.— Among narcotic plants 'loco weeds' are the most interesting. 'Loco' is a Spanish word meaning mad or crazy, and is applied in northern Mexico and southern United States to certain plants which so affect the brain of animals as to give them all the symptoms of brain disease. As described in the important papers of Chestnut[2] the weeds called 'loco' belong to genera of the bean family. "For many years," this writer observes, "a disease called loco, affecting cattle, horses, and sheep, has been generally known to the stockmen of the western ranges. This disease has most commonly been attributed to the action of certain plants, more rarely to that of alkali. Several species of plants have been suspected of producing the loco condition in animals and have been called loco plants or loco weeds and also crazy weeds from the nature of the disease. Nearly all of the plants which have been considered loco weeds belong to two genera of the pea family, Astragalus and Aragallus. These genera are represented by numerous species on the Western stock ranges.... (p. 87).... From a general description given of the loco disease it is apparent that this condition might very justly be termed a perverted appetite.... The horse and the sheep are the animals

[1] "Problems in the Chemistry and Toxicology of Plant Substances." *Science*, n. s., vol. 15, no. 391, June 27, 1902, pp. 1016–1028.

[2] Chestnut, V. K. "Preliminary Catalogue of Plants Poisonous to Stock." *Ann. Rep. Bur. of Anim. Indus., 1898*, pp. 403, 404.

which are most frequently affected by loco disease. Cattle occasionally acquire the loco habit, but the cases are comparatively rare. In certain parts of Montana the habit became so widespread among horses that the raising of them was abandoned until the locoed animals were disposed of and other horses which had not the loco habit had been imported" (p. 89). "During the progress of field work in Montana in 1900, about 650 locoed sheep and 150 locoed horses were seen"[1] (p. 90).

Mechanically Dangerous Plants.—There occur in Montana occasional losses of stock from plants acting mechanically. For example, the sharp-barbed awns of the porcupine grass (*Stipa spartea*) and squirreltail (*Hordeum jubatum*) when the plants are maturing, separate, and entering the mouth, throat, eyes, and ears of stock, affect the tissues and give rise to ulcers which cause intense suffering and necessitate killing.[2] Similarly the corn-stalk disease is sometimes attributed to malnutrition or impaction of the alimentary canal.

In this connection may also be cited an observation recorded by Thistleton-Dyer[3] which happens to bear upon the life of goats. "The introduction of the sweet briar into New South Wales, Australia, in many parts of which it is naturalized, affords a striking illustration of the mode in which the balance of nature may be disturbed in a wholly unforeseen way....The fruit of the sweet briar (*Rosa rubiginosa*) consists of a fleshy receptacle lined with silky hairs which contains the seed-like carpels.....The hairy linings of the fruit caused the death of a number of goats by forming hairy calculi, which mechanically occluded the lumen of the bowels. These goats were put on the land with the idea that they would eat down the briars and ultimately eradicate them, but the briars came out best and eradicated the goats. The cattle running on the land are also very fond of the briar berries, and

[1] Chestnut, V. K., and Wilcox, E. V. "The Stock-Poisoning Plants of Montana: A Preliminary Report." *U. S. Dept. of Agric. 1901*, bull. 26, pp. 87–90.

[2] Chestnut, V. K. "The Stock-Poisoning Plants of Montana. A Preliminary Report." *U. S. Dept. of Agric., 1901*, bull. 26, pp. 50–51.

[3] "The Sweet Briar as a Goat-Exterminator." *Nature*, vol. 66, no. 1697, May 8, 1902, p. 31.

from time to time one will die, and on *post mortem* [examination] no pathological changes can be found in any of the organs, nor do the hairy calculi appear in them, although their various stomachs are one mass of the briar seeds."

Living Environment. Insect Life

The features of physical environment such as moisture and desiccation, forestation and deforestation, heat and cold, cannot be considered by themselves or solely in relation to plant life but in relation to the insect life which they condition and which indirectly becomes the barriers and even the exterminators of mammalian life.

We may first consider the influence of the introduction into habitual feeding grounds of various forms of insect life which render these grounds practically uninhabitable and either kill or drive the animals out. Thus Wallace[1] observes: "The next case I will give in Mr. Darwin's own words: 'In several parts of the world insects determine the existence of cattle. Perhaps Paraguay offers the most curious instance of this; for here neither cattle nor horses nor dogs have ever run wild, though they swarm southward and northward in a feral state; and Azara and Rengger have shown that this is caused by the greater numbers, in Paraguay, of a certain fly which lays its eggs in the navels of these animals when first born. The increase of these flies, numerous as they are, must be habitually checked by some means, probably by other parasitic insects. Hence, if certain insectivorous birds were to decrease in Paraguay, the parasitic insects would probably increase; and this would lessen the number of the navel-frequenting flies — then cattle and horses would become feral, and this would greatly alter (as indeed I have observed in parts of South America) the vegetation: this again would largely affect the insects, and this, as we have just seen in Staffordshire, the insectivorous birds, and so onward in ever-increasing circles of complexity....'"

The two-horned rhinoceros (*R. bicornis*) of Africa as well as

[1] Wallace, Alfred R. *Darwinism*, 1889, p. 19.

some members of the antelope family are well known to be protected from insects by birds (see Millais's *Breath of the Veldt*, and other works). Anyone who has watched the sufferings of cattle and horses from flies knows that insects may become an important factor in expelling animals from a certain country to which they are naturally adapted by their tooth and foot structure.

Ticks.—Ticks, even when non-infection-bearing, form absolute and effective barriers to the introduction of quadrupeds into certain regions. In certain forested portions of South and Central America they endanger human life. In certain regions of Africa ticks are practically fatal to horses; as observed by Dr. D. G. Elliot thousands of ticks would sometimes gather on a horse as a result of a single night's grazing. The mane especially serves to collect these pests. Thus the falling mane of the northern horse is distinctly disadvantageous as compared with the upright manes of the asses and zebras. Ticks are capable of driving certain types of animals entirely out of a country and of indirectly causing certain modifications of the hair and epidermis.

Frontal Air Sinuses.—Larvæ invading the frontal sinus of the skull are not to be left out of account among the possible causes of elimination. An old trapper and close observer in British Columbia, Mr. Charles Smith, informs me that both the wild sheep of the region (*Ovis montana*) and the wapiti (*Cervus canadensis*) are seriously affected and sometimes killed by inflammation caused by these larvæ. The over-crowded caribou of Labrador and Newfoundland suffer from a fly which lays its eggs in the nostril passages.

In certain of the Eocene Titanotheres, in Dolichorhinus especially, the frontal air sinuses communicate with sinuses extending completely back to the occiput. The invasion of such sinuses by larvæ would undoubtedly be very harmful if not fatal.

Insects and the Food Supply.—The periodic devastations of certain insects especially those caused by locusts as cited by Lyell in Europe, Arabia, India, and Northern Africa, are quite sufficient to cause the extinction of certain species. As Lyell concludes:[1] "The occurrence of such events at certain intervals, in hot countries,

[1] Lyell, C. *Principles of Geology*, vol. 2, 1872, p. 445.

like the severe winters and damp summers returning after a series of years in the temperate zone, may affect the proportional numbers of almost all classes of animals and plants, and probably prove fatal to the existence of many which would otherwise thrive there; while, on the contrary, the same occurrences can scarcely fail to be favourable to certain species which, if deprived of such aid, might not maintain their ground."

(To be continued)

A PRELIMINARY STUDY OF THE FINER STRUCTURE OF ARCELLA

JOSEPH A. CUSHMAN AND WILLIAM P. HENDERSON

This study of Arcella is based upon two species, *Arcella vulgaris* Ehrenberg and *Arcella mitrata* Leidy. The structure of the test in Arcella is usually described as given by Leidy ("Fresh-water Rhizopods of North America," *U. S. Geol. Surv. Territories*, vol. 12, p. 167): "Composed of a more or less translucent or transparent chitinoid membrane, with a minutely hexagonal cancellated

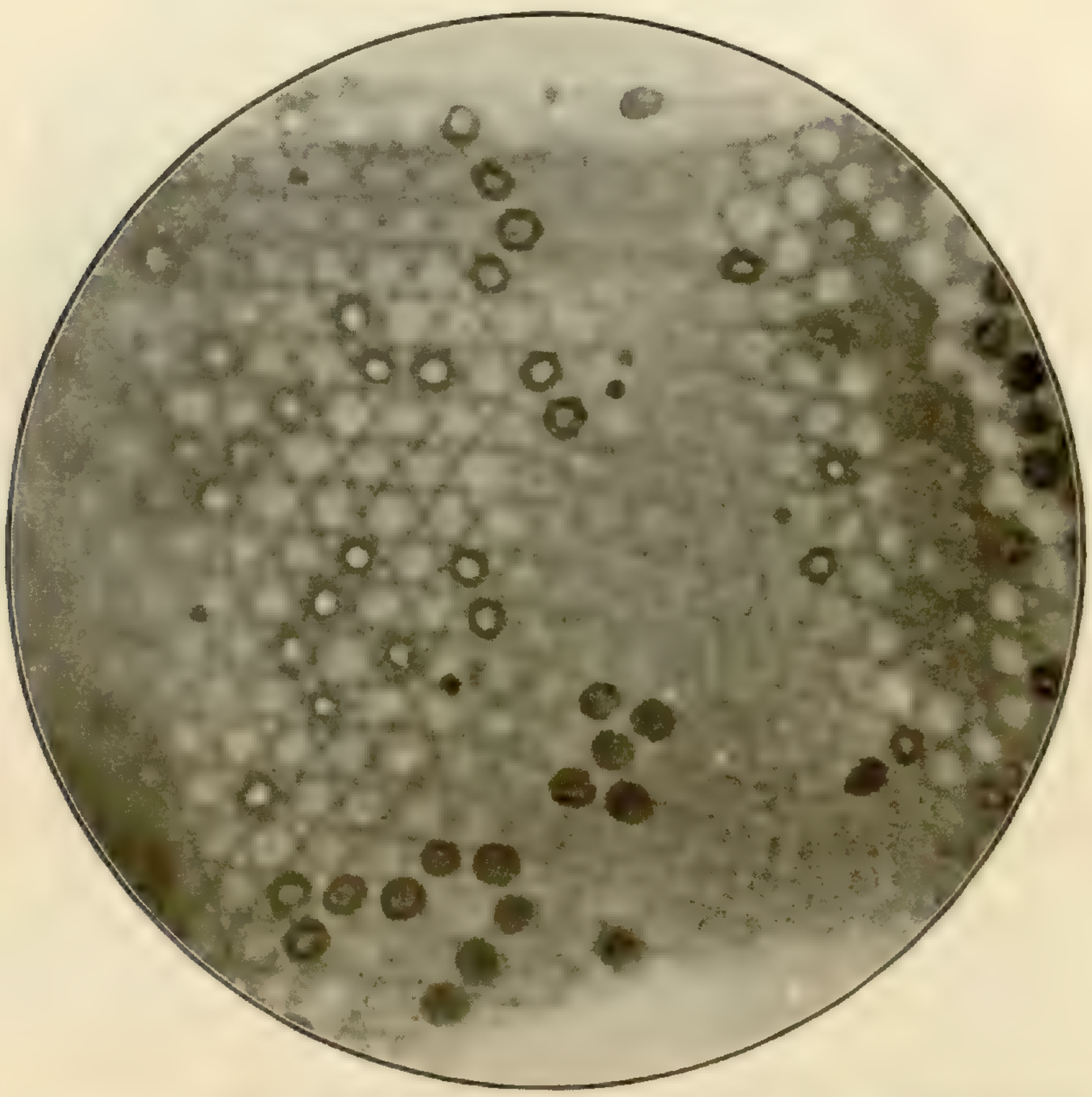

FIG. 1.— *Arcella vulgaris* Ehrenberg. ×3100. Showing many air bubbles in the cancelli and the structure of the network. Photomicrograph, $\frac{1}{12}$ in. oil-immersion objective.

structure." Closer study of the test of these two species with high magnification shows further complication of this structure, not shown at all in the "honeycomb" figure given by Leidy, Pl. 27,

Fig. 35. Moreover, as will be shown later, the arrangement of the hexagons is on an entirely different plan from that shown in Leidy's figure and those of other authors.

Hertwig and Lesser (*Arch. f. mikr. Anat.*, vol. 10, suppl., 1874) after reviewing and rejecting the conclusions of Dujardin, Ehrenberg, Claparède, Carter, and Wallich go rather fully into the more minute structure of the test and reach a positive conclusion as follows (p. 96): "Ihrer feineren Structur nach besteht die Schale aus zwei Platten, einer äusseren und einer inneren, welche einander parallel gelagert sind und durch ein bienenwabenartiges, hexagonale Figuren bildendes Fachwerk vereint werden"

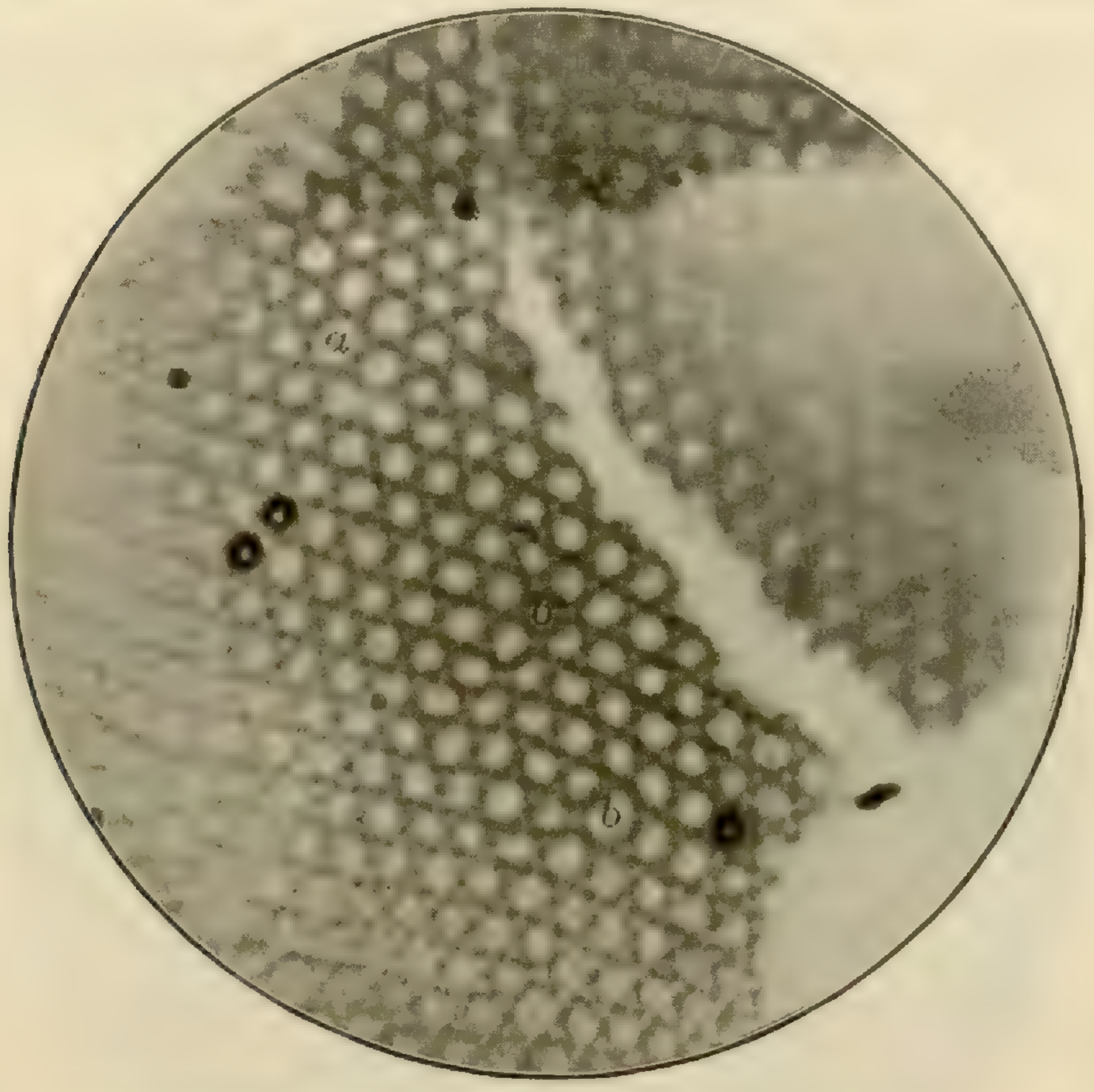

FIG. 2.— *Arcella vulgaris* Ehrenberg. ×3100. Showing the introduction of columns of plates and resulting change in the number of sides of the plates. *a*, heptagonal plate; *b*, *b*, irregularities with more than one column initiated.

Hertwig and Lesser, by treatment of the test with sodium carbonate and acetic acid induced the formation of bubbles of carbonic-acid gas in the cancelli, which they considered closed chambers. In our specimens many bubbles of air were introduced into the cancelli with the greatest ease in the following manner. From about the entire test, under low power, the water was

drawn away until its level was so reduced that air reached the specimen. Bubbles at once formed in some of the cancelli and were present after dehydrating, clearing, tearing in pieces, and mounting in balsam or styrax. Many of these air bubbles are seen in Fig. 1, and a few are scattered about in Fig. 2. The ready entrance of air to form bubbles in the cancelli hardly seems to bear out the view that there are two thin plates, with the cancellated network lying between, as Hertwig and Lesser thought. If there were two membranes, it would be impossible, by the simple method adopted in this work, to cause air bubbles to form in the closed chambers lying between them. That there is but one membrane is very strongly indicated by the present study.

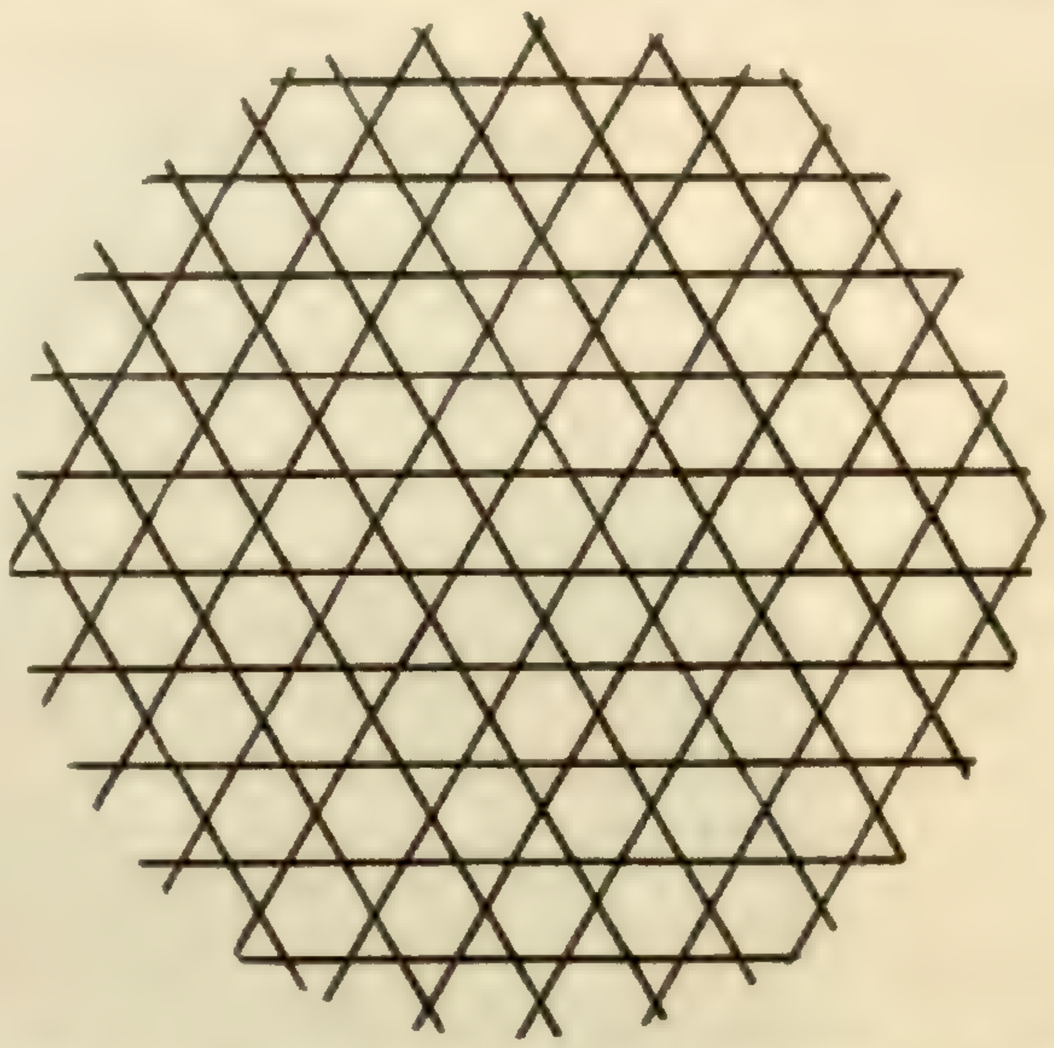

FIG. 3.— Diagrammatic representation of the structure of the upper surface of the network.

The next thing to determine was the position of the single membrane, whether it is on the outer or the inner side of the network. In the introduction of air bubbles the specimens were placed with the mouth-opening downward, the shell cavity being filled with water. At no time was the water allowed to become low enough to permit air to enter the mouth. In this manner only the upper surface was exposed, and no air could have entered the cancelli from the inside. Moreover, had air entered the shell cavity, it would at once have become evident as a large air bubble at the upper part of this cavity. The introduction of air having been thus controled, we conclude that the bubbles formed on the outside of the membrane, and therefore that the raised pattern or network projects externally.

The form of this network, as has been said, is radically unlike the honeycomb structure heretofore assigned to it. It is, to be sure, hexagonal in its main features, but the arrangement of the hexagonal areas is not at all what it has been represented. In the honeycomb arrangement the hexagons have sides in common.

In the Arcella test the hexagons have no sides in common. Instead, the hexagonal areas are so placed that the three adjacent sides of three neighboring areas enclose a small triangular space. Just here we find a further complication of the structure. These interpolated triangles are not solid portions of the network, but themselves contain areoles of subtriangular outline. The density of the medium through which the light is transmitted seemed, with the best illumination obtainable, the same in the small triangular areoles as in the larger hexagonal areas. From this we concluded that the areoles are depressed areas in the network

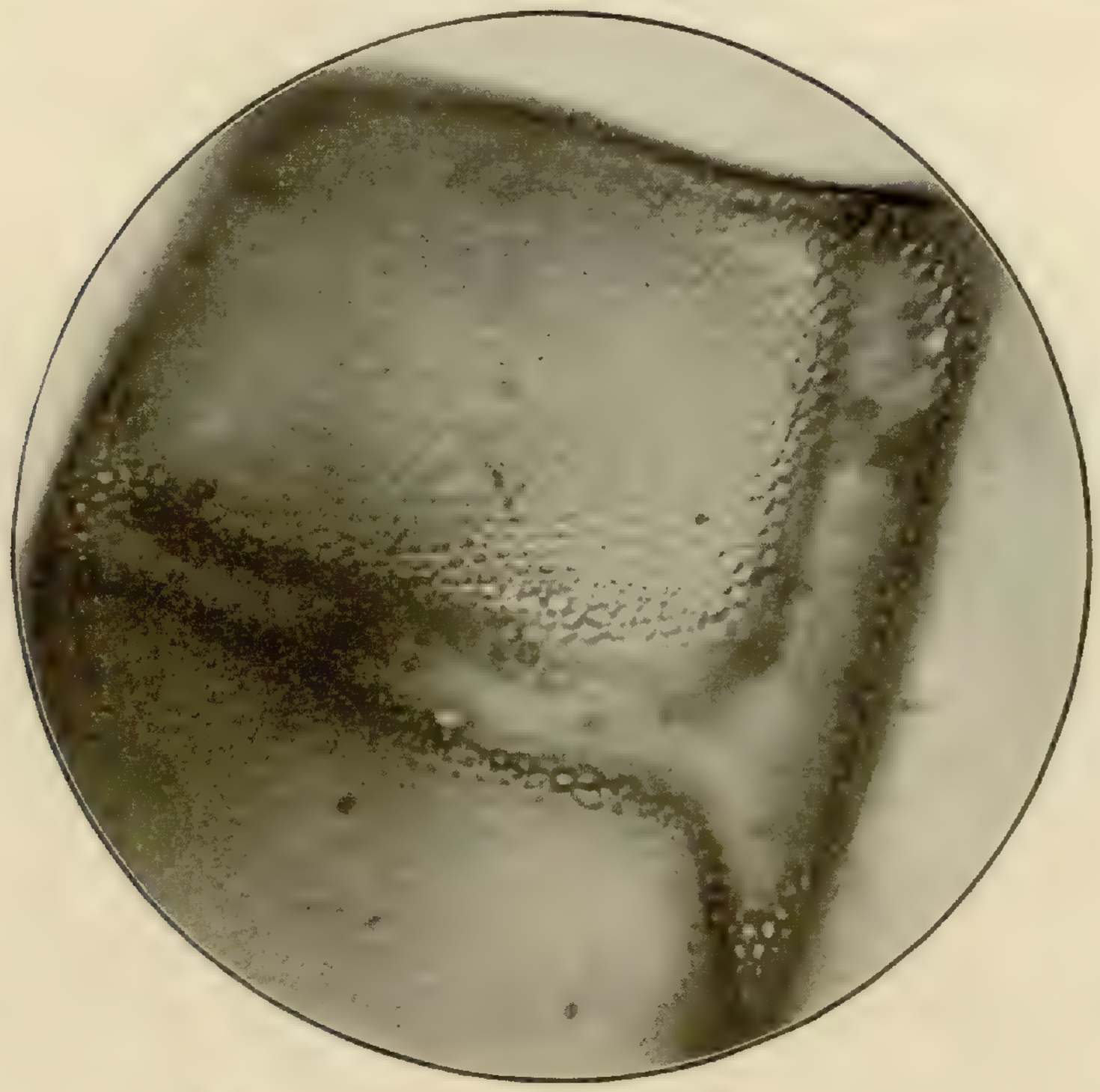

FIG. 4.— *Arcella mitrata* Leidy. ×1200. Photomicrograph showing structure of network like that in *A. vulgaris*.

similar, except in point of size and shape, to the hexagonal areas. Diagrammatically then, the network may be conceived as formed of straight lines in three sets of parallels, the lines of each set making an angle of sixty degrees with those of the two other sets (see diagram, Fig. 3). A comparison with the actual photographs, especially Fig. 2, seems to bear out this conclusion. That no air bubbles formed in the smaller spaces is natural, since the surrounding areas are much larger and of equal depth.

When the test was seen in optical section the reason for the view that there are two membranes was apparent, for the limiting upper edges of the raised network give the appearance of a wall covering in the top. This appearance seems to be merely the effect of refraction of light. The basal membrane may be clearly seen. In general the height of the raised network above the basal membrane is about equal to the width of the hexagonal areas.

Besides the further complication of structure in the test, another

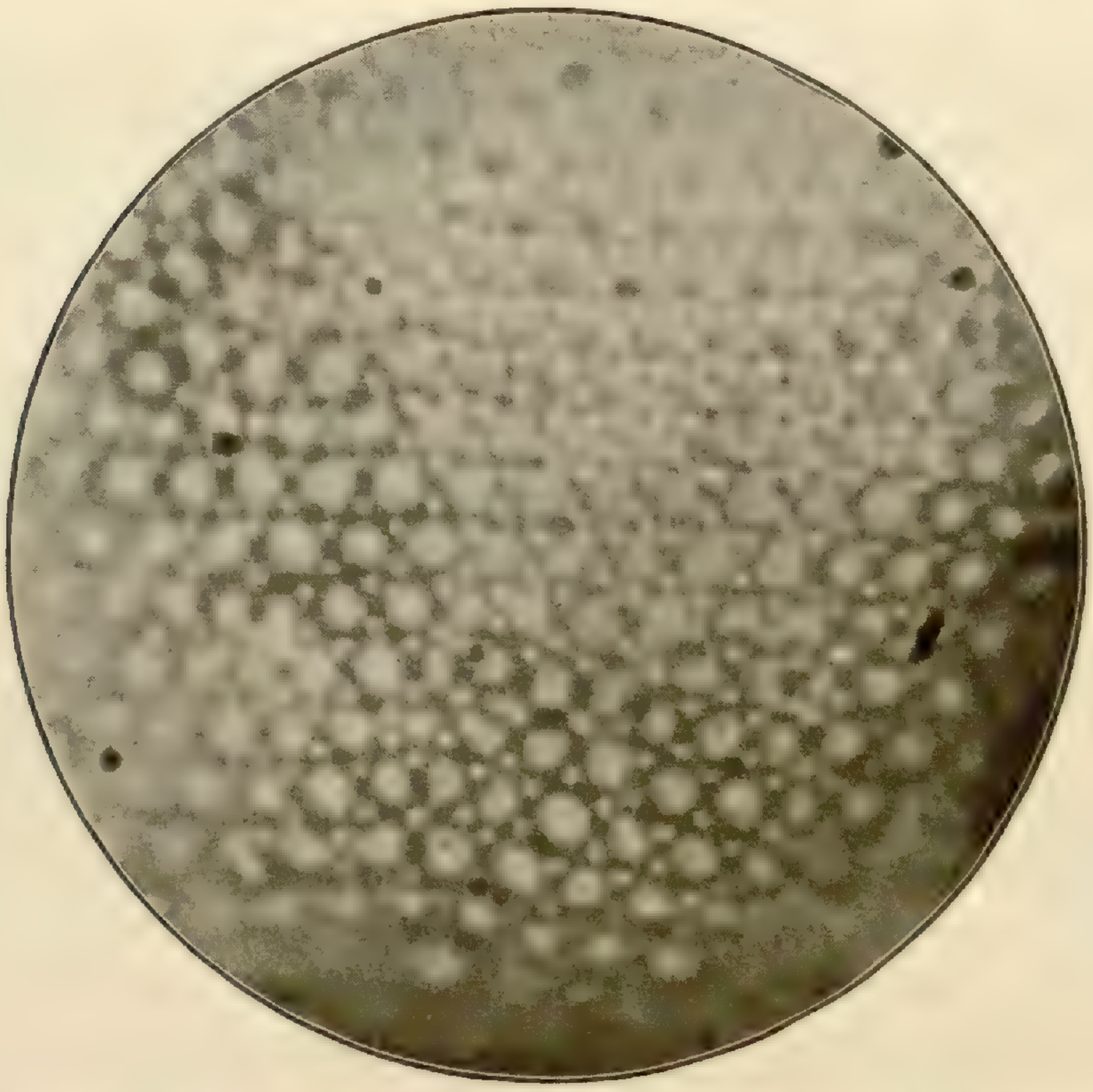

FIG. 5.— *Arcella mitrata* Leidy. ×3300. Photomicrograph of a portion of the specimen shown in Fig. 4, but much enlarged.

series of observations was made on the method of growth of the shell. As the animal increases in size toward the periphery, this increase must in some way be provided for. An increase in size of the hexagons might have been used but this would have been detrimental to the plan of structure. Instead of this, new columns of hexagonal areas are added or interpolated among the previous ones. By this means the plan of structure is not seriously interfered with. These new columns may be added in any of three directions conforming to the directions of the three sets of parallel lines already referred to.

In typical cases the new column of plates is initiated by an area having but five instead of six sides. To compensate for this mechanically, the preceding area has seven sides (Fig. 2, *a*). This equating method of heptagons and pentagons is typical whenever a single column is added in one spot. In certain cases, however, more than one column may originate, even with the same area, and then various irregularities are taken on (Fig. 2, *b*). In such cases, areas with but four sides are met with occasionally instead of the normal pentagonal areas. Besides this variation in the number of sides of the areas in different portions there seems to be a definite alternation of the columns, to the right and left of the axis in which they are added. This applies of course only to those columns added successively in one of the three directions mentioned above.

Altogether, the test of Arcella is far from the simple hexagonal structure figured by Leidy and other authors. Its complexities are worthy of further study and comparison with the tests of other rhizopods.

NOTES AND LITERATURE

ASTRONOMY AND PHYSICS

A Laboratory Astronomy.[1] — This book is the outcome of the author's experience in handling with his large elementary classes in Harvard College, "those difficult and discouraging" parts of astronomy which deal with "the diurnal motion of the heavens and the apparent motions of the sun, moon, and planets among the stars." It is suggested that each student ought to make for himself, and discuss carefully, a great number of simple observations, so that the facts to be brought out may become a part of his own experience. The apparatus required, most of which has been especially designed for this work, is so inexpensive that each student can be supplied with a complete outfit. This makes it possible for all the members of a class to do similar work at a given time — "a principle of cardinal importance in elementary laboratory work with large classes." The book is intended primarily for teachers and should be used in connection with a descriptive text-book.

No one who knows Professor Willson personally, will need the reviewer's assurance of the remarkable ingenuity of his methods, or of the admirable qualities of his style. This book is a fine example of a modern tendency, new in astronomy, but fortunately well established in physics and chemistry, of carrying interesting laboratory work into the very beginning of a student's acquaintance with natural science.

A feature of interest to the general reader is a well written chapter on the contents and use of a nautical almanac, with a full set of specimen pages.

H. N. D.

A Laboratory Physics.[2] — This book, like the one just reviewed, is intended as a laboratory manual for a large elementary course in Harvard College, and presents such material as might form a set of

[1] Willson, Robert W. *A Laboratory Astronomy.* Boston, Ginn and Co., 1906. 8vo, ix + 189 pp.

[2] Sabine, Wallace C. *A Student's Manual of a Laboratory Course in Physical Measurements.* Rev. ed., Boston, Ginn and Co., 1906. 8vo, vi + 97 pp.

"daily lectures preceding the laboratory work and describing the experiments to be performed." It is, nevertheless, remarkable for its freedom from the pedantic, cut-and-dried, schedule method of presentation which so frequently characterizes elementary laboratory manuals, for many of Professor Sabine's pages are interesting reading as such, and throughout, "too specific instruction" has been avoided as tending "not only to deprive the student of initiative but also to make any departure in the apparatus confusing."

As a matter of fact the spirit of the book would have been better expressed by reversing the order of these two clauses, for "in the majority of cases the description is purposely not such as will admit of a mechanical and unintelligent interpretation." In particular, the three-page introduction is an unusually fine presentation of the point of view from which a student should attack the work which is to follow.

The experiments described are representative of nearly the whole range of elementary physics. They should properly be preceded by the still more elementary work of a modern high-school course, as much of the apparatus requires comparatively skilful and appreciative handling. Two short appendices on "significant figures" and "graphical representation" are especially worthy of mention.

H. N. D.

BIOLOGY

Clements's Research Methods in Ecology [1] is the outcome of some eight years of practical work by the author in the experimental study of the factors that determine the distribution and adaptive modifications of plants. Students of this comparatively new branch of science are to be congratulated on the possession in this volume, of a concise statement of the aims, methods, and problems of ecology. The author points out that the greater part of so called ecological study has hitherto been very superficial and of comparatively little value, largely because of a failure to recognize and measure accurately the several factors that determine for each species its particular environment.

[1] Clements, F. E. *Research Methods in Ecology.* Lincoln, Neb., University Publishing Co., 1905. 8vo, xvii + 334 pp., 85 figs.

The subject matter is considered under four main heads. Chapter I is devoted to a general statement of the scope of ecology. Chapter II deals with habitat, and contains a description of the instruments and methods used in recording water-content, light-intensity, temperature, soil, and other factors upon which the organism is dependent. Many of the methods described, have been elaborated by the author in his own extensive work in the West. Chapter III, the Plant, considers the general relations, adaptations, and reactions of the separate organism, while Chapter IV deals with the Formation in its various aspects, and the methods of studying the relations that groups of plants bear to one another and to their environment.

This work should do much towards establishing ecology and experimental plant evolution upon a firmer basis by pointing out the need and the method of making absolute determinations of factors, instead of the inaccurate generalizations so often recorded. The time is also not far distant when it will be a simple matter to determine, by an examination of a given soil in a given situation, what plants are best adapted to any portion of a single farm, so that agriculture may be carried on under much more precise regulations.

Although plants alone are dealt with in the present volume, many of the methods described will have to be used in a more exact study of animal habitats, and here lies a large field as yet hardly more than touched upon. The author recognizes the zonal distribution of continental forms, and proposes a new nomenclature for these as occurring in North America. Apparently, however, the areas already recognized and named by American zoölogists are ignored, and the new classification given, does not seem as adequate as that now in use by the latter.

A glossary, including numerous terms proposed by the author, and a bibliography of plant ecology complete the book. Notwithstanding the very detailed statement of contents, the lack of an index is a disadvantage.

G. M. A.

Moore's Universal Kinship [1] is intended as a protest against that attitude of the human mind that would conceive all animals other than man as man's just and legitimate prey. The author appears to have become greatly impressed by Darwin's conception of the

[1] Moore, J. H. *The Universal Kinship.* Chicago, Chas. H. Kerr and Co., 1906. 12mo, x + 330 pp. $1.00.

ultimate consanguinity of all sentient beings, and addresses himself to the task of arousing in man a greater feeling of sympathy for his fellow creatures. The argument falls under three heads: man's physical relation to other animals, his psychical similarity to them in certain fundamental ways, and hence his ethical kinship. The author concludes that the fact "that vertebrate animals, differing in externals as widely as herring and Englishmen, are all built according to the same fundamental plan, with marrow-filled backbones and exactly two pairs of limbs branching in the same way, is an astonishing coincidence"; hence the fancied superiority of the human race is but a figment of man's mind for "man is not a god, nor in any imminent danger of becoming one."

While agreeing with the author that "the art of being kind" is in sore need of cultivation among us, one cannot but be amused at the mixture of fact and error, observation and travelers' tales, seriousness of statement and straining after absurd expressions, that characterizes this not unreadable book.

G. M. A.

ZOÖLOGY

Pratt's Vertebrate Zoölogy.[1]— In continuation of the plan of his *Invertebrate Zoölogy*, published some three or four years ago, Dr. Pratt now offers a similar guide to the dissection of vertebrates, which would appear to merit the same favorable reception accorded to the earlier volume. As a guide to vertebrate dissection its chief claim to usefulness over the already existing laboratory manuals on the subject lies perhaps in the fact that it includes under one cover those forms most frequently employed in American laboratories, for descriptions of which the teacher or student has formerly found it necessary to refer to two or three separate works. Outlines are furnished for the dissection of seven types, *viz.*: dogfish, perch, mud-puppy (Necturus), frog, turtle, pigeon, and cat. Of these, that of Necturus will probably be especially acceptable, since it is a form commonly

[1] Pratt, Henry Sherring. *A Course in Vertebrate Zoölogy. A Guide to the Dissection and Comparative Study of Vertebrate Animals.* Boston, Ginn and Co., 1905. 8vo, x + 299 pp.

employed for laboratory work in connection with courses on comparative vertebrate anatomy, and heretofore no published outline for its dissection has been generally accessible.

The question as to the practical and pedagogical value of manuals of this nature remains, as before, an individual one with different teachers. In respect to method of treatment the present outlines offer few innovations; but apparently the attempt has been made to have them as practical as possible, so that they may, if it is desired, be placed in the student's hand with little or no modification. To this end the descriptions are made rather fuller than some instructors might consider desirable, especially those who believe that laboratory outlines should consist merely of a framework of directions as to the method of proceeding to work, together with suggestive questions, rather than a description of what the student is expected to see. Dr. Pratt has largely overcome this objection by the relatively great number of original drawings called for. Satisfactory drawings insure that the student has seen what is described, and the omission of all illustrations from the book will make him dependent upon his own observations in supplying these.

L. J. C.

Stephens's California Mammals[1] is a handbook written to popularize the study of the rich mammalian fauna of that State. In addition to a brief description of each species with a statement of its distribution, the author has given a number of field notes on the forms that have come under his personal observation. The accounts of the Cetacea are taken from Scammon as the author has had no experience with them. The nomenclature used for these animals is in some cases not that now in vogue. The scientific names of the species considered, are followed by the name of the authority as usual, but the author tells us that he has omitted the parentheses in all cases where they are usually employed. This seems a mistake in a work of this sort. The chapter on life zones is accompanied by a chart showing the location of these areas. A check-list and glossary are followed by a very complete index. Several rather characterless wash drawings serve as full page illustrations.

The work can be but preliminary, the author states, but undoubtedly it will be of value as a basis for a more thorough investigation.

G. M. A.

[1] Stephens, F. *California Mammals.* San Diego, Cal., West Coast Publishing Co., 1906. 8vo, 351 pp., illus. $3.50.

Ichthyological Notes.—In the *Bulletin of the Bureau of Fisheries* (vol. 25, 1905), Dr. Barton W. Evermann has a beautifully illustrated memoir on the "Golden Trout of the High Sierras." In small streams tributary to Kern River, along the flanks of Mount Whitney are found small trout, very gorgeously colored, with brilliant golden and orange shades on the bodies and fins. These colors harmonize with the orange colors of the underlying rocks. Recently Dr. Evermann, at the request of President Roosevelt, conducted an investigation of these trout. He finds them probably descended from the Kern River Trout (*Salmo gilberti* Jordan), but modified in size, in coloration, and in the reduction of the scales. From the Kern River Trout, the Golden Trout are separated by impassable waterfalls. But still more remarkable is the fact that in each of the three different streams thus isolated, there is a different type or species of Golden Trout. Besides the original species, *Salmo aguabonita* Jordan, from South Fork of Kern River, Evermann describes two new species, closely allied to this, but each sprung independently from the same parent stock. These species are: *Salmo roosevelti* Evermann, from Volcano Creek, and *Salmo whitei* from Soda Creek.

It is not certain whether the vivid colors of each of these three species are protective, due simply to natural selection, or whether to some more obscure influence acting on all individuals in these mountain brooks. The paper is illustrated by paintings by Charles B. Hudson and by maps and photographs of the waterfalls and streams within the habitat of the Golden Trout.

In the same *Bulletin* for 1904, Dr. Charles Wilson Greene of the University of Missouri has published his studies of the physiology of the Chinook Salmon, a species of especial interest from the fact that every individual dies after reproduction.

In the *Smithsonian Miscellaneous Collections*, 1905, vol. 48, Mr. Barton A. Bean gives an account of the Whale Shark (*Rhinodon typicus*), the largest of the sharks, a specimen of which has been lately taken on the coast of Florida. The same shark has been described from the Gulf of California as *Micristodus punctatus*, and lately from Japan as *Rhinodon pentalineatus*.

In the same number, Dr. Theodore Gill gives an essay on the Cyprinoid fishes, with figures of numerous species and a discussion of the vernacular names current in England and America.

In the *Proceedings of the Washington Academy of Science*, Robert E. Snodgrass and Edmund Heller record the fishes taken about the

Galapagos Islands by the Hopkins-Stanford Expedition of 1898; 184 species are recorded, with synonymy and valuable notes on their characters and geographical distribution. The new species has been described in a previous paper.

In the same *Proceedings*, Mr. William F. Allen, also of Stanford University, describes in great detail the lymphatic system in the large Californian Sculpin or Cabezon, *Scorpænichthys marmoratus*.

In the *Proceedings of the Royal Society of Edinburgh*, Dr. Louis Dollo describes the abyssal fish, *Bathydraco scotiæ*.

In the *Proceedings of the Biological Society of Washington* (1905) Dr. Seth E. Meek, records a collection of fishes from the Isthmus of Tehuantepec. *Cichlasoma zonatum*, from Oaxaca, is described as new. Dr. Meek also describes two new species, *Pimelodella eigenmanni* from Sao Paulo, Brazil, and *Anisotremus williamsi* from Santos.

In the *Proceedings of the Philadelphia Academy* for 1905, Mr. Henry W. Fowler discusses a collection of ninety species of fishes from the Baram Basin in Borneo. Most of these are fresh-water species, several new genera and species being described. One goby, *Gigantogobius jordani*, allied to Eleotris, reaches a length of 26 inches.

Numerous papers in the *Annals and Magazine of Natural History* by C. Tate Regan, treat of fishes. The following matters may be noted: Regan records the European shark, *Hexanchus griseus*, from Japan and concludes that the Californian species, *Hexanchus corinus* is not distinct from it. He gives reviews of various groups of South American fishes, especially Cichlidæ and Loricariidæ. A new white-fish, *Coregonus gracilior*, is described from the Lakes of Cumberland. A monographic review of the family Galaxiidæ is given by Mr. Regan in the *Proceedings of the Zoölogical Society of London*.

Dr. George A. Boulenger, as President of the Zoölogical Section of the British Association for the Advancement of Science (1905), discusses in illuminating fashion the distribution of African fresh-water fishes. In the *Annals and Magazine of Natural History*, July, 1905, Dr. Boulenger gives a list of the fresh-water fishes of Africa with the distribution of each species. In the *Proceedings of the Zoölogical Society*, he records the fishes of Lake Chad. All the species are common both to the Nile and the Niger, a fact which indicates that a connection between these rivers formerly existed through Lake Chad.

In the *Scientific Investigations of the Fisheries of Ireland*, for 1905, Messrs. E. W. L. Holt and L. W. Byrne, give a "First Report on the Fishes of the Irish Atlantic Slope." A new species is *Melamphaës eurylepis*. *Nettophichthys retropinnatus* of Holt is shown to be the young of the eel, *Synophobranchus pinnatus*. The genus Myctophum in this paper is called by the much later name of Scopelus.

Professor Keinosuke Otaki, and his associates, Fujita and Higurashi, continue their beautifully illustrated work on the fishes of Japan. In the third issue are included the Kurodai (*Sparus schlegeli*), the Maguro, or Tunny (*Thunnus schlegeli* = ? *Thunnus thynnus*), the Maiwashi or Japanese Sardine (*Sardinella melanosticta*), the Konoshiro (*Konosirus punctatus*), and the Common Goldfish or Funa. The press work in this series is beautifully done, and the text is accurate and helpful.

In the *Journal of the College of Science* (vol. 20, 1905) of the Imperial University of Tokyo, Shigeho Tanaka has an account of two new species of Japanese Chimæras. It is a remarkable fact that of the ten known living species of this ancient and extraordinary genus, five are known from Japan only, and the center of distribution of each of these is Sagami Bay, which is the first indentation south of the Bay of Tokyo. Mr. Tanaka describes *Chimæra jordani* and *Chimæra owstoni* as new species, in addition to the three, *Chimæra phantasma*, *Chimæra mitsukurii*, and *Chimæra purpurascens* already described from the waters about Misaki. When we consider the number of rare or ancient sharks recorded from this region, the extraordinary richness of the Bay of Sagami in shark-like types becomes very apparent. It was from Sagami Bay that Garman obtained Chlamydoselachus and Mitsukuri the "Goblin Shark," called Mitsukurina. In the same bay is a Rhinachimæra, a Heterodontus, and many species of Squaloid sharks, one of them with luminous areas on the body.

Other Japanese sharks are described by Garman in the *Bulletin of the Museum of Comparative Zoölogy* (vol. 46, 1906). These are: *Parmaturus pilosus*, *Centrophorus acus*, *Centrophorus tessellatus*, *Acanthidium rostratum*, *Acanthidium aciculatum*, and *Centroscymnus owstoni*. To Parmaturus, the Japanese species, *Pristiurus eastmani*, is also referred, as also *Catulus xaniurus* from California. Garman refers the genus Deania to the synonymy of Acanthidium and Zameus to that of Centroscymnus. *Squalus uyatus* of Italy is referred to Centrophorus. Garman describes *Hemigaleus pectoralis*, as a new species from the New England Coast.

Japanese fishes are also discussed in several papers in the *Proceedings of the United States National Museum* for 1905. Jordan and Seale describe six new species from different parts of Japan, the most notable being a new genus, Sayonara, near Anthias. The fishes of the islands of Yaku and Tanega, as collected by Robert V. Anderson, are recorded by Jordan and Starks. Seven of these, mostly blennies, are figured as new. Jordan and McGregor describe as new, the Japanese Threadfin or Agonashi, *Polydactylus agonasi*. Jordan reviews the sand-lances of Japan, and Jordan and Snyder review the sturgeons. An elaborate paper on the many species of flounders and soles of Japan is by Jordan and Starks. Jordan and Herre review the Japanese herrings, and Snyder the Japanese surmullets. Jordan and Snyder discuss the Giant Bass of Japan, *Stereolepis ischinagi*, a species closely related to the California Jewfish, and *Erilepis zonifer*, the huge Aburabodzu or Fat-priest of Japan. This species was first known from a single specimen taken by Lockington in the Bay of Monterey.

Jordan and Snyder discuss the killifishes of Japan, and also the Chinese loaches of the genus Misgurnus. The fishes of Shanghai are discussed by Jordan and Seale, and those of Port Arthur by Jordan and Starks. Among the latter is a remarkable new genus of gobies, Ranulina, with the teeth fringe-like about the rim of the mouth.

Mr. Edwin C. Starks reports on the collection of fishes made in Ecuador and Peru, by the late Mr. Perry O. Simons, a most promising Stanford student, conducting explorations for the British Museum, who was murdered by highwaymen in Bolivia in 1899. In the same *Proceedings*, Dr. Evermann and H. W. Clark describe three new species from Santo Domingo, *Platypœcilus perugiæ*, *Platypœcilus dominicensis*, and *Sicydium buscki*. Eugene W. Gudger discusses the breeding habits and embryology of a species of pipe-fish, *Syngnathus floridæ*.

In the *Proceedings of the Davenport Academy of Sciences* (vol. 10, 1905), the memorial volume dedicated to Mrs. Putman, the honored patron of the Academy, Jordan and Seale discuss the fishes of Hong Kong. This paper is beautifully illustrated, two of the plates being colored.

In the *National Geographic Magazine*, 1905, Dr. Hugh H. Smith treats in detail of the Japanese fisheries.

In the *Zoölogisches Jahrbuch* for 1905, is a paper by the late Professor Franz Hilgendorf of Berlin on fishes from East Africa.

Dr. Robert Collett, in the *Forhandlinger Videnskabs Selskab* of Christiania for 1905, continues his monographic reviews of the fishes of Norway.

In the *Pacific Monthly*, Portland, April, 1906, Jordan describes in popular fashion the trout and salmon of the Pacific, with drawings by Sekko Shimada.

In the *Popular Science Monthly* for April, 1906, Jordan records the occurrence in considerable numbers at Avalon in Southern California, of the Japanese Hirenaga or Yellow-fin Albacore, *Germo macropterus*. This large game fish, known by its citron yellow finlets occurs also in Hawaii.

In the Paris *Bulletin d'Histoire Naturalle*, Dr. Jacques Pellegrin discusses the fishes of Lake Baikal, known as Cottocomephorus.

In the *Journal of Sciences of Lisbon*, 1904, Dr. Balthazer Osorio has a catalogue of the fishes of Cape Verde, and in the same journal are various notes on other fishes.

In the *American Naturalist* (vol. 39, 1905), Miss Julia Worthington discusses the Myxinoids or hag-fishes, as studied by her at the Stanford Seaside Laboratory at Pacific Grove. Miss Worthington rejects the genus Polistotrema, detached from Eptatretus (which she calls by the much later though more familiar name of Bdellostoma), regarding the number of gills as having barely specific importance. The separation into genera may be questionable, but there is as yet no adequate reason for placing all these variant forms in a single species, an arrangement first suggested by Dr. Howard Ayers.

In the *Bulletin of the American Museum of Natural History*, Mr. L. Hussakof gives a valuable account of the structure of two species of Dinichthys. In the *American Journal of Science*, Dr. C. R. Eastman makes a strong argument in favor of the dipnoan affinities of the Arthrodires. He goes far towards placing Woodward's view of the case on a sound foundation. The contention of Eastman rests largely on the intimate relationship of the dipnoan Neoceratodus to the Arthrodires on the one hand and to characteristic dipnoans on the other, the living genus Neoceratodus being more primitive than either of the extinct types with which it is compared. Dr.

Eastman does not believe that dipnoans are descended from Crossopterygians, but rather that they may have come from the Pleuracanthus-like sharks. The association of the Arthrodires with the Dipneusti, finally disposes of the group of Placodermata, in which the Arthrodires were associated with the Ostracophores.

In the *Bulletin of the University of Montana*, Dr. James A. Henshall gives a list of the scant fish fauna of Montana, 36 species being represented, with notes on the game fishes represented or introduced into the State.

In the *Hawaiian Forester* (vol. 2, 1905), Mr. Alvin Seale gives an account of the successful introduction from Galveston to Honolulu of three species of mosquito-eating killifishes. These are *Mollinesia latipinna*, *Fundulus grandis*, and *Gambusia affinis*. These fishes were received in fine condition, and they have shown great avidity in freeing Hawaii of her worst insect pest.

In the *American Journal of Physiology*, 1905, Professor G. H. Parker discusses the stimulation of the integumentary nerves of fishes by light. The sensitiveness to light of the vertebrate skin is established. This trait may have served as a basis from which the retinal structures and the temperature sense were derived.

In the *Marine Biological Association Report* (vol. 1, 1903), are elaborate studies of the Plaice, *Pleuronectes platessa*. Dr. William Wallace has investigated the growth rate of the species. Walter Garstang reports on the topographical distribution of the species. A number of studies on the natural history of the Plaice are recorded in German by Mr. Garstang in *Rapports du Conseil International pour l'Exploration de la Mer*, 1905.

In *Ergebnisse der Schwedischen Südpolar Expedition* (vol. 5, 1905) Dr. Einar Lönnberg describes and figures numerous new Antarctic fishes. Lönnberg also furnishes (*Kong. Vet. Aarsbog*, 1906) biographical sketches of the Swedish ichthyologists, Petrus Artedi and the late Fredrik Adam Smith (1839-1904).

In the *Archivos do Museo Nacional do Rio de Janeiro* (vol. 13, 1906), Alipio de Miranda Ribeiro records the vertebrates of Itatiaya, Brazil, and gives a review of the species of the Characin genus Megalabrycon.

In the *Journal of Anatomy and Physiology*, Mrs. Onera A. M. Hawkes of the University of Birmingham describes the important

discovery of a vestigial sixth branchial arch in the shark, Heterodontus. As in the more primitive groups of Hexanchidæ and Chlamydoselachidæ, there are six or seven gill arches, this discovery of six arches in the still more ancient group of Heterodontidæ, the oldest of existing sharks, is a matter of much interest and importance. The number five found in all other recent sharks is apparently a matter of specialized reduction.

In the *Annals of the New York Academy of Sciences*, 1906, Dr. Raymond C. Osburn makes a strong and convincing argument for the theory of the origin of the vertebrate limbs from fin folds. Dr. Osburn contends that paired and unpaired fins in fishes are similar structures and that the evidence is overwhelmingly in favor of the origin of all fins as local outgrowths from the body wall.

DAVID STARR JORDAN

BOTANY

Leaf Structure.—A paper by Mrs. Clements,[1] which contains a historical review of the work previously done along similar lines, is based upon observations made on some 300 species growing under the varied conditions presented by the Colorado foothills and the mountains of the Pike's Peak region of the Rocky Mountains. The conclusions arrived at support the views now generally held as to the influence of local conditions upon the histological structure of leaves, and are based upon exceedingly extensive and precise measurements relating to water-content of soil, humidity, light, and temperature, all of which factors are brought into relation with the histological structure of stem leaves. Thanks to the system of classification adopted as well as to the numerous comparative tables, the reader, at a glance, is able to note with exactitude the influence of each of the factors upon leaf structure, in which he is aided by a large number of excellent illustrations.

The statement: "Full sunlight is equally strong throughout the regions, and not more intense for high altitudes, as is generally supposed" [p. 28] is to be noted, in view of Professor Wiesner's recent conclusions to the contrary.

H. HUS

[1] Clements, E. S. "The Relation of Leaf Structure to Physical Factors." *Trans. Amer. Micr. Soc.*, 1905, pp. 19–102, 9 pls.

Light Intensity.— Professor Wiesner [1] now gives a detailed account of his measurements of light intensities, made chiefly in the Yellowstone Park, and reaches the conclusion that, with a clear sky, the intensity of the total daylight as well as that of the direct sunlight increases with the elevation above sea level, while the intensity of the diffused light decreases with increasing elevation but constant altitude of the sun. He further finds that the diffused light, in the course of the day, does not increase correspondingly to the increase of direct sunlight.

The greater intensity of the total daylight on the surface of the sea as compared to that on the main land, Professor Wiesner ascribes to the greater amount of light reflected by water surfaces.

H. Hus

Bilancioni's Dictionary.[2]— A capital model of a modern botanical dictionary is afforded by a little book recently published in the Italian language. Histology, anatomy, morphology, physiology, and the biology of plants are indicated among the topics treated, and 111 pages are given to a biographic account of distinguished botanists. The treatment of the several entries ranges from a mere indication of equivalence in the case of synonymous words to four pages (including a classification) for fruit, two and a half for germ-plasma, three and a half for protoplasm, eleven for tissues, etc. Plant names do not appear; but common Latin adjectival forms on which specific names have frequently been framed, are defined, and throughout the derivation of terms is given.

W. T.

Notes.— A little pamphlet of 109 pages, by Professor Bessey, has been issued by the University Publishing Company, of Lincoln, Nebraska, under the title *Elementary Botany*. Laboratory and field instructions are followed by a terse manual of the common genera of Nebraska plants.

One of the most attractive of recent elementary text-books is Miss

[1] Wiesner, J. "Beiträge zur Kenntnis des photochemischen Klimas des Yellowstone-Gebietes und einiger anderer Gegenden Nord Amerikas." *Denkschr. d. math. naturw. Kl., kaiserl. Akad. d. Wissensch., Wien*, vol. 80, 1906.

[2] Bilancioni, G. *Dizionario di botanica generale*. Milano, Hoepli, 1906. 16mo, xxi + 926 pp. 10 lire.

Stoneman's *Plants and their Ways in South Africa.* Familiar facts are supplemented by (to us) unfamiliar illustrations.

Some new plants from the Canadian Rockies and Selkirks are described by Miss Farr in *The Ottawa Naturalist* for August.

Vol. 7 of Engler and Drude's *Vegetation der Erde* is devoted to a part of West Australia, treated by Diels.

Chevalier gives an illustrated account of Adansonia in no. 6 of the current volume of the *Bulletin de la Société Botanique de France.*

Mr. A. D. E. Elmer has begun the publication, at Manila, of a new serial under the title *Leaflets on Philippine Botany.* The first number, dated April 8, is devoted to a paper on Philippine Rubiaceæ, by the editor.

Goodale has a note on the persistence of Calluna in Massachusetts in *The American Journal of Science* for August.

Viguier publishes the results of an anatomico-systematic study of Araliaceæ in ser. 9, vol. 4, nos. 1–3, of the *Annales des Sciences Naturelles, Botanique,* issued in July.

The flowering of *Agave palmeri* and *A. lecheguilla* is reported in the *Journal of the New York Botanical Garden* for August.

Aloe campylosiphon is figured by Berger in *Die Gartenwelt* of August 11.

Showers of conifer pollen in Mexico, and its accumulation on the water in the crater of Toluca, are recorded by Urbina in vol. 3, no. 7, of the *Anales del Museo Nacional de Mexico.*

An account of the poisoning of horses by *Equisetum arvense* is given by Peters and Sturdevant in the *19th Annual Report of the Agricultural Experiment Station of Nebraska,* which also contains a paper on a disease of the Cottonwood due to *Elfringia megaloma,* by Heald, and a study of the relation of early maturity to hardiness in trees, by Emerson.

The second supplement to vol. 1 of *The Philippine Journal of Science,* issued on June 15, is devoted to descriptions and figures of new Philippine ferns, by Copeland.

A fully illustrated article on fern buds is published by Kupper in *Flora* of July 25.

Evans contributes some notes on Japanese Hepaticæ to the *Proceedings of the Washington Academy of Sciences* for August.

A monograph of Swiss Myxomycetes, by Schinz, has been separately issued from Heft 6 of the *Mitteilungen der naturwissenschaftlichen Gesellschaft* in Winterthur, for 1906.

Portraits of Bateson and several other well known plant breeders or botanists are published in *The Gardeners' Chronicle* of August 4.

MacDougal discusses discontinuous variation in pedigree culture in *The Popular Science Monthly* for September.

Earle publishes a considerable paper on Cuban fungi, with numerous half-tone illustrations, in the *Primer Informe Anual de la Estación Central Agronómica de Cuba*, bearing date of June 1.

A scholarly study of *Jugendformen und Blütenreife im Pflanzenreich*, by Diels, has been issued from the Borntræger press of Berlin, as an attractively printed, well illustrated pamphlet of 130 pages.

The double number of the *Botanische Zeitung* issued on July 15 is devoted to a paper by Vöchting on regeneration and polarity in the higher plants.

A study of the fall of the terminal buds, characteristic of certain trees, is separately issued by Tison from the *Bulletin de la Société Linnéenne de Normandie* for this year.

Details of experimental studies of the effect of frost on trees are given by Soranes in vol. 35, no. 4, of the *Landwirtschaftliche Jahrbücher*, issued in July.

A series of six well illustrated articles on the differentials of trees in winter was published by Professor Weed in the issues of *Forest and Stream* between January 6 and March 31, of this year.

A short appreciative note on Burbank is printed by de Vries in *The Independent* of May 17.

An illustrated account of the botanical garden of Cambridge, England, is given by Zahu in *Die Gartenwelt* for August 18.

An instructive discussion of variations in animals and plants is contributed by Jordan to *The Popular Science Monthly* for June.

An account of de Vries and his critics is given by Gager in *Science* of July 20.

A somewhat radical analysis of plant study and nomenclature is published by C. F. Baker in *Science* of May 25.

A plea for the proper use of "mega" and "macro" in terminology and nomenclature is published by Chamberlain in *Science* of May 25.

Papers on the flora of the Amazon region are being published by Huber in current issues of the *Boletim do Museu Goeldi* of Pará.

A list of the Bryophytes and higher plants — so far as determined — of the Lamao Forest Reserve is published by Merrill as vol. 1, supplement 1, of *The Philippine Journal of Science*; and a discussion of the vegetation of the Reserve, by Whitford, is contained in nos. 4 and 6 of the same volume.

A third part of de Wildeman's "Enumeration des plantes récoltées par Emile Laurent....pendant sa dernière mission au Congo," issued in June from the Vanbuggenboudt press of Brussels, reaches p. 354 and pl. 106.

Vol. 4, part 4, and vol. 5, part 3, of Wood's *Natal Plants* have recently been issued, bringing the former volume to completion.

Further studies of the botany of Kerguelen, St. Paul, and New Amsterdam are being published by Schenck in the *Wissenschaftliche Ergebnisse der deutschen Tiefsee Expedition* of the *Valdivia*.

The seed and seedling of *Trollius albiflora* are described by Ramaley in *University of Colorado Studies* for March.

Further additions and changes are made in Eschscholtzia by Fedde in late numbers of *Repertorium Novarum Specierum*.

Professor Greene, in his *Leaflets* of June 5, expresses a belief in the existence of some hundreds of species of acaulescent violets in the United States, and a disbelief in the existence of any hybrids in the group.

An economic account of *Erodium cicutarium* in Arizona, by Thornber, forms *Bulletin no. 52* of the Agricultural Experiment Station of that Territory.

The genus Neobrittonia is proposed by Hochreutiner, in vol. 9 of the *Annuaire du Conservatoire et du Jardin Botaniques de Genève*, for the reception of *Sida acerifolia* Lag.

A large increase in the species of Ptelea is noted by Greene in vol.

10, part 2, of *Contributions from the U. S. National Herbarium*, issued in July.

Hybridization in Eucalyptus is analyzed by Maiden in vol. 10 of the *Report of the Australasian Association for the Advancement of Science*, recently distributed.

Piqueria, Ophryosporus, Helogyne, and other Eupatoriaceous Compositæ are the subject of new series 32 of "Contributions from the Gray Herbarium of Harvard University," by Robinson, which appears as vol. 42, no. 1, of *Proceedings of the American Academy of Arts and Sciences*.

An illustrated monograph of Epilobium, by Léveillé, is being published in the *Bulletin de l'Académie Internationale de Géographie Botanique*.

A revision of 17 genera of North American Vernonioid Compositæ, by Gleason, has been separately issued from vol. 4, no. 13, of the *Bulletin of the New York Botanical Garden*.

A third paper on Canadian Antennarias is published by Greene in *The Ottawa Naturalist* for July.

Rhododendron vaseyi is figured in *Curtis's Botanical Magazine* for June.

An economic account of the mango and its diseases in Hawaii, by Higgins, forms *Bulletin no. 12* of the Hawaiian Agricultural Experiment Station.

A good account of the pecan and its varieties is given by Hume in *Bulletin no. 85* of the Florida Agricultural Experiment Station.

A mammoth plant of *Anthurium veitchi* is figured in *Möller's Deutsche Gärtner-Zeitung* of June 2.

A comprehensive thesis on the "Scobiform" seeds of orchids and other plants, by Hirt, forms no. 30 of the *Mitteilungen aus dem botanischen Museum der Universität, Zürich*.

An illustrated account of the cultivation and preparation of fiber from Phormium is given by Fulton in the *Annual Report* for 1905 of the New Zealand Department of Agriculture.

An important account of certain Indian bamboos is being published by Brandis in current issues of *The Indian Forester*.

Endlich gives an economic account of "Zacaton," — species of Epicampes, — in *Der Tropenpflanzer* for June.

The synonymy of *Eriophorum chamissonis* is discussed by Holm and Fernald in *The Ottawa Naturalist* for June.

Illustrations of the curious Karasaki specimen of *Pinus thunbergii* are given by Miyoshi on plates 29 and 30 of his *Atlas of Japanese Vegetation.*

A short illustrated account of *Sequoia sempervirens* is given by Elliott in *Forest Leaves* for June.

Morphological notes on Cycads are published by Seward in vol. 13, part 5, of the *Proceedings of the Cambridge Philosophical Society.*

Part 3 of Grout's *Mosses with Hand-Lens and Microscope* bears date June, 1906.

An account of the morphology of the fern stem, illustrated by *Dennstædtia punctilobula,* is published by Conard in no. 187 of the *Johns Hopkins University Circular.*

A monograph of Scapania, forming a quarto volume of 312 pages, with 52 plates, has been published by Müller as vol. 83 of the *Nova Acta der k. Leop.-Carol. deutschen Akademie der Naturforscher.*

A revision of the Chareæ of North America, by C. B. Robinson, is separately printed from vol. 4, no. 13, of the *Bulletin of the New York Botanical Garden.*

Part 2 of Holway's *North American Uredineæ* deals with species of Puccinia found on Moraceæ, Santalaceæ, Aristolochiaceæ, Polygonaceæ, Amarantaceæ, Portulacaceæ, Caryophyllaceæ, Cruciferæ, Saxifragaceæ, Crassulaceæ, and Rosaceæ. A notable feature of the work is the frequent illustration, by photo-micrographs from type material, of species reduced to the status of synonyms.

The effect of symbiotic fungi in the germination of Odontoglossum is illustrated by Bernard in *The Orchid Review* of July.

A contribution to a revision of the North American Hydnaceæ, by Banker, forms vol. 12, no. 2, of the *Memoirs of the Torrey Botanical Club.*

A preliminary list of some 500 higher fungi collected about St. Louis has been published by Glatfelter in vol. 16, no. 4, of the *Transactions of the Academy of Science of St. Louis.*

Further infection experiments with *Erysiphe graminis*, confirming the current conclusions as to its physiological differentiation on different hosts, are recorded by Reed in a paper separately printed from vol. 15, part 1, of the *Transactions of the Wisconsin Academy of Sciences, Arts, and Letters*.

Salmon figures the Venturias and associated Fusicladiums of apple and pear in *The Gardeners' Chronicle* of July 14.

Glæosporium psidii is shown by Sheldon, in *Bulletin 104* of the West Virginia University Agricultural Experiment Station, to develop an ascigerous stage pertaining to the genus Glomerella,— on the paraphyses of which he has a note in *Science* of June 1.

An illustrated paper on the fungi of scale insects is published by Parkin in vol. 3, part 1, of the *Annals of the Royal Botanic Gardens*, Peradeniya.

An account of fungi and plant diseases, by Clinton, forms part 5 of the *Report of the Connecticut Agricultural Experiment Station for 1905*.

A large number of foliar acarodomatia are described by de Wildeman in vol. 30, no. 2, of the *Annales de la Société Scientifique de Bruxelles*.

An extensive study of palm germination is published by Gatin in the *Annales des Sciences Naturelles, Botanique* of June.

A further account of acarodomatia is given by Borzi in vol. 4, no. 1, of *Contribuzioni alle Biologia Vegetale*, published from the Botanical Institute of Palermo.

Three ferns and 199 flowering plants which grow on trees (without being epiphytes) in parts of Italy are enumerated by Ugolini in the *Commentari dell' Ateneo di Brescia* for 1905.

The sand dunes of Guardamar, and the planting effected on them, form the subject of an illustrated paper by Mira in vol. 4, no. 1–2, of the *Memorias de la R. Sociedad Española de Historia Natural*.

Bruck gives an account of wind injury to foliage in Heft 1 of vol. 20, part 2, of the *Beihefte zum botanischen Centralblatt*.

The biology of a large number of Dicotyledons, from germination to flowering, is traced and illustrated by Sylvén in the recently issued vol. 40, no. 2, of the *K. Svenska Vetenskapsakademiens Handlingar*.

Apogamy is recorded for *Dasylirion acrotrichum* by Went and Blaauw in a separate from the Proceedings of February 24 of the *K. Akademie van Wetenschappen te Amsterdam.*

The conditions which effect the time of the annual flowering of fruit trees are analyzed by Sandsten in *Bulletin no. 137* of the University of Wisconsin Agricultural Experiment Station.

Britton and Viereck publish an extensive record of the insect visitors of orchard flowers in part 4 of the *Report of the Connecticut Agricultural Experiment Station for 1905.*

Mattei gives an account of pollination in Cupuliferæ (of which Castanea, Castanopsis, and Pasania are entomophilous) in vol. 4, no. 1, of the *Contribuzioni alla Biologia Vegetale* of the Botanical Institute of Palermo.

Graenicher contributes pollination notes to the April *Bulletin of the Wisconsin Natural History Society.*

Photograms of common weed seeds found with grass and clover seed are given by Garman in *Bulletin no. 124* of the Kentucky Agricultural Experiment Station.

An illustrated paper on common weeds and their eradication, by Wilson, forms *Bulletin no. 95* of the University of Minnesota Agricultural Experiment Station.

Notes on charcoal and on rubber and gutta-percha, with especial reference to the Philippines, form respectively *Bulletins no. 2 and 3* of the Bureau of Forestry of those islands.

Altamirano contributes an extensive illustrated paper on "guayule" to the May *Boletín de la Secretaria de Fomento* of Mexico.

A number of papers on the constituents of medicinal plants are published in the recently issued vol. 53 of the *Proceedings of the American Pharmaceutical Association.*

A number of northwestern plants are figured, in an economic connection, by Nelson in *Bulletin no. 73* of the Washington Agricultural Experiment Station.

An attractive little tree book, with half-tone illustrations, by Correvon, has been issued by the Atar Company, of Geneva.

Harshberger publishes on phytogeographic influences in the arts and industries of American aborigines in the April *Bulletin of the Geographical Society of Philadelphia.*

A special subscription edition of Bailey and Miller's *Cyclopedia of American Horticulture* has been issued by Doubleday, Page and Co., of New York, in six volumes bound to match their "Nature Library." To what was said of the first edition, from 1900 to 1902, in the *Naturalist* need only be added that the present (fourth) edition contains corrections of detected errors and a conspectus of families and genera prepared by Mr. Miller, while the number of illustrations has been greatly increased.

Under the title *Hortus Veitchii*, Mr. J. H. Veitch has privately printed a sumptuous quarto history of the great plant house of which he is now the head,which is of interest especially for the biographic sketches of its many explorers and hybridists and the remarkable list of plants originated or introduced to European gardens by them. Numerous excellent illustrations add to its attractiveness.

A portrait of Hollós forms the frontispiece to the *Journal of Mycology* for May.

A biographic sketch, with portrait, of C. C. Parry, is contributed to the July number of the *Annals of Iowa* by C. A. White.

A new relief portrait of Rumphius is figured in *Bulletin no. 34 van het Koloniaal Museum te Haarlem.*

The Journals.— *Botanical Gazette*, May: — Elmer, "New and Noteworthy Western Plants — III"; Bergen, "Some Littoral Spermatophytes of the Naples Region"; House, "New and Noteworthy North American Species of Trifolium"; Lewis, "The Basidium of *Amanita bisporigera.*"

Botanical Gazette, June: — Wiegand, "Some Studies Regarding the Biology of Buds and Twigs in Winter"; Yamanouchi, "The Life History of *Polysiphonia violacea*"; Weiss, "The Structure and Development of the Bark in the Sassafras"; Hill, "The Distribution and Habits of some Common Oaks."

Botanical Gazette, July: — Jeffrey and Chrysler, "On Cretaceous Pitoxyla"; Shantz, "A Study of the Vegetation of the Mesa Region East of Pike's Peak: The Bouteloua Formation"; Nelson, "Contributions from the Rocky Mountain Herbarium — VII"; Peirce, "Anthoceros and its Nostoc Colonies"; Hill, "Distribution and Habits of some Common Oaks."

The Bryologist, July: — Fink, "Further Notes on Cladonias — VII"; Collins, "Mounting Mosses, Some Hints"; Hayne, "A List of Hepatics Collected in the Vicinity of Little Moose Lake.... Herkimer Co., N. Y."; Smith, "A List of Mosses Collected on the Adirondack League Club Tract, Herkimer Co., N. Y."; Merrill, "Lichen Notes no. 3, Chemical Tests in Determining Lichens"; Gilbert, "Two Anomalies and a Curious Sight."

Bulletin of the Torrey Botanical Club, May: — Cardiff, "A Study of Synapsis and Reduction"; Cockerell, "Fossil Plants from Florissant, Colorado"; House, "Studies in the North American Convolvulaceæ — I."

Bulletin of the Torrey Botanical Club, June: — Kirkwood, "The Pollen-Tube in Some of the Curcubitaceæ"; Cushman, "New England Desmids of the Sub-Family Saccodermæ."

Bulletin of the Torrey Botanical Club, July: — Spalding, "Absorption of Atmospheric Moisture by Desert Shrubs"; Reed and Smoot, "The Mechanism of Seed Dispersal in *Polygonum virginianum*"; Gleason, "The Pedunculate Species of Trillium."

Fern Bulletin, July: — Klugh, "The Fern Flora of Ontario"; McNeill, "*Botrychium biternatum*"; Palmer, "Green and Red Stiped Lady Ferns"; Clute, "The Moonwort"; Lee, "The Hart's Tongue in Tenn."; Davenport, "The Forms of *Botrychium simplex*"; "A Check-list of the North American Fernworts (*continued*)"; Druery, "*Lomaria spicant bipinnatum* in America."

Iowa Naturalist, January: — Cratty, "Notes on the Iowa Sedges — I"; Anderson, "Additions to the Flora of Decatur County, Ia."; "The Flora of Lake Wabonsie"; Fitzpatrick, "The Iowa Gentians."

Journal of Mycology, March: — Kellerman, "Job Bicknell Ellis" (*with portrait*); Bates, "Rust Notes for 1905"; Saccardo, "Micromycetes Americani Novi"; Bubak, "Einige neue Pilze aus Nord America"; Bessey, "*Dilophospora alopecuri*"; Sumstine, "*Pleurotus hollandianus* sp. nov.," "Notes on *Wynnea americana*"; Ricker, "Second Supplement to New Genera of Fungi Published since the Year 1900, with Citations and Original Descriptions"; Kellerman, "Index to North American Mycology," and "Notes from Mycological Literature — XVIII."

Journal of Mycology, May: — Shear, "*Peridermium cerebrum* and *Cronartium quercuum*"; Morgan, "North American Species of Heli-

omyces"; Ricker, "Second Supplement to New Genera of Fungi Published since 1900, with Citation and Original Description"; Kellerman, "Index to North American Mycology," and "Notes from Mycological Literature — XIX."

Annals of the Carnegie Museum, July: — Jennings, "Additions and Corrections to the List of the Vascular Flora of Allegheny County, Pa."; "A New Species of Kneiffia"; "A Note on the Occurrence of *Triglochin palustris* in Pa."; and "A New Species of Ibidium (Gyrostachys)."

Journal of the New York Botanical Garden, May: — Britton, "Recent Botanical Explorations in Porto Rico."

Journal of the New York Botanical Garden, June: — Murrill, "A Serious Chestnut Disease"; Britton, "A Large Oak Struck by Lightning."

Journal of the New York Botanical Garden, July: — Nash, "The Flowering of Queen Victoria's Agave."

Journal of the New York Botanical Garden, August: — Maxon, "Report on a Collecting Trip in Costa Rica"; Shreve, "A Winter at the Tropical Station of the Garden."

Muhlenbergia, vol. 1, no. 9, July 30: — Osterhout, "Colorado Notes"; Heller, "Western Species, New and Old — VI."

The *Yearbook* of the U. S. Department of Agriculture for 1905, recently issued, contains the following articles of botanical interest: — Webber, "New Fruit Productions of the Department of Agriculture"; Langworthy, "Fruit and its Uses as Food"; Shamel, "The Effect of Inbreeding in Plants"; Rolfs, "New Opportunities in Subtropical Fruit Growing"; True, "Progress in Drug-Plant Cultivation."

The Ohio Naturalist, May: — Claassen, "Key to the Species of Liverworts Recognized in the Sixth Edition of Gray's Manual of Botany"; Kellerman and York, "Additions to the Flora of Cedar Point — I."

The Ohio Naturalist, June: — Schaffner, "Terminology of Organs in Various Conditions of Development"; Jennings, "Additions to the Flora of Cedar Point — II"; Young, "Key to the Ohio Viburnums in the Winter Condition"; Griggs, "A Diurnal Rotation in Leaves of Marsilea."

The Plant World, May: — Andrews, "Some Monstrosities in Trillium"; Harper, "A December Ramble in Tuscaloosa Co., Ala."; Wiegand, "The Passage of Water from the Plant Cell during Freezing."

The Plant World, June: — Cook, "The Disintegrating Influences of Tropical Plants"; Osterhout, "On the Mountain Top"; Bowman, "The Chinese Sumach, or Tree of Heaven,— *Ailanthus glandulosa*"; Harris, "Apparently Imparipinnate Leaves in Cassia."

Rhodora, May: — Lamson-Scribner, "Notes on Trisetum and Graphephorum"; Fernald, "Some Anomalous Plants of Tiarella and Mitella"; Knight, "Some Notes on our Yellow Cypripediums"; Blanchard, "Two New Species of Rubus from Vermont and N. H."; Knight, "Some New Records of Maine Plants"; Holm, "Remarks upon Mr. House's Paper on *Pogonia verticillata*."

Rhodora, June: — Fernald, "*Paronychia argyrocoma* and its New England Representative"; Collins, "New Species, etc., Issued in the Phycotheca Boreali-Americana"; Sanford, "A Station for *Asplenium ebenoides* in Mass."; Davenport, "The Apetalous Form of *Arenaria grœnlandica* on Mt. Mansfield"; Fernald, "A New Variety of *Carex interior*"; Knight, "*Viola novæ-angliæ* in the Penobscot Valley."

Rhodora, July: — House, "The Violet Hybrids of the District of Columbia and Vicinity"; Collins, "Notes on Algæ — VII"; Fernald, "Some New or Little known Cyperaceæ of Eastern North America"; Collins, "Preliminary Lists of New England Plants — XIX" [Buxbaumiaceæ, Georgiaceæ, and Polytrichaceæ].

Torreya, May: — Shreve, "A Collecting Trip at Cinchona"; Barnhart, "Chloronyms"; Berry, "Pleistocene Plants from Virginia."

Torreya, June: — Rusby, "A Historical Sketch of the Development of Botany in New York City"; Harper, "Some More Coastal Plain Plants in the Palæozoic Region of Alabama"; Blanchard, "Two New and Somewhat Anomalous Blackberries"; Eastwood, "The Earthquake and the California Academy of Sciences"; Mackenzie, "*Ranunculus sicæformis*"; House, "A Note upon *Ipomœa cuneifolia*."

Torreya, July: — Rusby, "A Historical Sketch of the Development of Botany in New York City" (*continued*); Greene, "Doctor Torrey

and Downingia"; Blanchard, "Two New Dewberries of the *hispidus* Group"; Britton, "*Galactia odonia*"; House, "A New Southern Convolvulus."

Torreya, August: — Douglas, "The Rate of Growth of *Panæolus retirugis*; Rydberg, "Bassekia or Rubacer"; Rose, "*Terebinthus macdougali*, a New Shrub from Lower California"; House, "Notes on Southern Violets — I."

University of Colorado Studies, June: — Cockerell, "The Fossil Fauna and Flora of the Florissant (Colorado) Shales"; Ramaley, "Plants of the Florissant Region in Colorado."

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DEVOTED TO THE NATURAL SCIENCES
IN THEIR WIDEST SENSE

CONTENTS

		Page
I. The Causes of Extinction of Mammalia (Concluded)	PROFESSOR H. F. OSBORN	829
II. The Alpine Flora of Colorado	PROFESSOR T. D. A. COCKERELL	861
III. Blood Gills of Simulium pictipes	DR. T. J. HEADLEE	875
IV. Publications Received		887

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THE

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THE CAUSES OF EXTINCTION OF MAMMALIA

(*Concluded*)

HENRY FAIRFIELD OSBORN

LIVING ENVIRONMENT. INFECTIOUS DISEASES AND INSECTS

In his *Great Rift Valley* (p. 265) Gregory observes that the great herds of game which roamed over the steppes of South Africa are being rapidly decreased in size and number. Man no doubt has played the leading part in the annihilation of the enormous herds that once thronged Cape Colony. The fact that during the last few years the game has retreated from the Somali coast into the interior shows how easily it can be driven from a district. In South Africa, however, man's influence has probably been insignificant as compared with natural agencies, lions and disease being the leading factors in extermination. Vast herds of the wild buffalo (*Bubalus caffer*) were exterminated between 1890 and 1893 by the cattle disease (rinderpest), which also killed off the gnu and giraffe (*op. cit.*, p. 266). Gordon Cumming[1] observed, as early as 1855, that " ....the goat in many districts is subject to a disease called by the Boers 'brunt sickta,' or burnt sickness, owing to the animals afflicted with it exhibiting the appearance of having been burnt. It is incurable; and if the animals inflicted are not speedily killed, or put out of the way, the contagion rapidly spreads, and it is not uncommon for a farmer to lose his entire flock with it. This sad distemper also extends itself to the *feræ naturæ*. I have shot hartebeests, black wilde-

[1] *The Lion Hunter in South Africa*, London, 1855, p. 138.

beests, blesbucks, and spring-bucks, with their bodies covered with this disease. I have known seasons when the three latter animals were so generally affected by it, that the vast plains throughout which they are found were covered with hundreds of skulls and skeletons of those that had died therefrom."

Aflalo [1] in his paper "The Beasts that Perish," has discussed many of the various causes of extermination and gives disease a prominent place. Among the Carnivora there are the non-epidemic diseases, such as distemper, affecting dogs, foxes, wolves, cats, and other wild felines. The more rare and sporadic epidemics claim victims among the Carnivora wholesale. The prevalence of rabies among foxes was observed on the continent from 1830 to 1838 in Switzerland, also in Württemberg and Baden.

Carnivora are protected by their relatively non-gregarious habits. On the contrary, the more gregarious Herbivora offer much more favorable conditions for the spread of disease. Flemming in his *Animal Plagues* enumerates 86 epidemics affecting wild quadrupeds and birds. In the list are diseases affecting nearly every wild species in Europe and some in the New World, including the red deer (*Cervus elaphus*), reindeer (*Rangifer tarandus*), the chamois (*Rupicapra tragus*), wild hog, also among the Carnivora, wolves, foxes, bears, among the Rodentia, the hares, rabbits, and rats. Various forms of tuberculosis account for a large percentage of death among domesticated animals. Only the goat enjoys immunity from it. Among animal plagues anthrax was formerly the most rapid and deadly, and is now perhaps the least common owing to Pasteur's discoveries. American zoölogists are familiar with the spread of disease from domesticated to non-domesticated animals, of the sheep scab, for instance, to the wild sheep (*Ovis montana*).

Insects and Infection.— In my opinion the most striking advance toward a complete theory of the causes of natural extinction has come from recent discoveries regarding the real nature of the animal diseases and how they are communicated. Only recently have we come thoroughly to understand that insects are the most

[1] The original article has not been accessible to the writer.

active means of introducing and spreading fatal diseases over great geographical areas and on a vast scale.

Moisture Favoring the Spread of Diseases Carried by Flies.—The presence of the blood protozoan parasites known as *trypanosomes*, combined with certain flies which act as disease carriers, is in many countries correlated with moist conditions. This is especially true of the disease known in India as 'surra,'[1] the history of which was first suspected by Surgeon Major Lewis in 1888.

Extermination of the Equidæ. Surra.—The wide geographical range of surra and related diseases is significant with reference to former periods in the history of the Equidæ. All authors now agree with Lewis that the disease is carried by flies and coincides with moist conditions occurring chiefly during or immediately after heavy rainfalls, though sporadic cases may occur at other seasons of the year. In the "Emergency Report on Surra" by D. E. Salmon and C. W. Stiles[2] this is described as chiefly a wet-weather disease, invariably fatal to horses and mules, occurring in other animals, such as camels and elephants, more rarely in ruminants, and transmissible to goats, sheep, and other mammals. In India it is said to affect horses, camels, and elephants (p. 18). It occurs in Burma, Persia, Tonquin, and Korea. In Africa there is the similar *nagana* or tse-tse fly disease, more accurately described below by Bruce[3] (p. 833). In Algiers, France, and Spain, the dourine or *maladie de coit* attacks the horse and ass in particular, and may be transmitted to certain other animals; it is attributed to a trypanosome, *T. equiperdum*. In the Philippines surra caused the death of 2000 army horses in six months. The intermediary is a fly, *Stomoxys calcitrans*. It was also reported (Curry, 1902) as affecting the carabao (*Bos* (*Bubalus*) *kerabau*), but according to Lingard ruminants are not particularly susceptible. An interesting note which may bear upon the *origin of colors* in certain quadrupeds is the advice to those in charge of horses in the Philippines (p. 97): "Avoid light colored animals as much

[1] Lewis, T. R. "Flagellated Organisms in the Blood of Animals." *Physiological and Pathological Researches . . . .of the late Timothy Richards Lewis*, 8vo, London, 1888.

[2] *U. S. Dept. of Agric., 1902, Bureau of Animal Industry*, bull. 42.

[3] *Science*, n. s., vol. 22, no. 558, Sept. 8, 1905, pp. 289–299.

as possible; the darker the animal the safer he appears to be from the attack of flies." In this connection we recall the dark color of the true Bovinæ. In South America the *mal de caderas* affects horses, asses, cattle, hogs, and certain other animals, and is attributed to the protozoan known as *Trypanosoma equinum*. It is distinctively a wet-weather disease, almost completely disappearing in dry seasons. Asses, swine, and water hogs are said to be affected, and horses are never known to recover. It is chronic in course, lasting from two to five months in horses, and from six to twelve in asses and mules. See Voges [1] for fuller details.

Immunity and Adaptation.— Existing conditions among the large quadrupeds of Africa are especially important because of the increasing conviction that North American conditions in the Oligocene, Miocene, and Pliocene are most closely paralleled in the great upland region of modern Africa, the central life belt as distinguished from the coast belt.

From these recent discoveries [2] it appears that *immunity from disease* is one of the most important features of animal adaptation to environment, and that conversely non-immunity has probably been one of the potent causes of diminution and extinction. T. H. Morgan [3] includes the phenomenon of immunity among the adaptive processes. He states, as his personal opinion, however, that certain of these phenomena could not be explained as due to any selective processes. Similarly Leo Loeb [4] believes that a large number of instances of acquired immunity cannot be directly explained as adaptive phenomena.

Variations in Immunity.— There are in Africa diseases fatal to both wild and domesticated animals, others fatal to domesticated animals to which wild animals are immune. Some to which all successive generations succumb; others to which immunity is acquired in the second generation or among 'natives.' Still more remarkable is the fact that both wild and domesticated

[1] "Das Mal de Caderas." *Zeitschr. f. Hyg. u. Infectionskrankh.*, vol. 39, (3) 13 März, pp. 323–372.

[2] *Nature*, vol. 72, no. 1872, Sept. 14, 1905, pp. 496–503. Address of Bruce, before the Section of Physiology, British Association.

[3] *Evolution and Adaptation*, New York and London, 1903.

[4] "Immunity and Adaptation." *Biol. Bull.*, August, 1905, p. 141.

'immunes' may act as reservoirs of disease organisms which through flies or ticks may be carried to non-immunes. Thus the wild ruminants of Africa among the Bovidæ especially, the buffalo (*Bos* (*Bubalus*) *caffer*), the kudu (*Strepsiceros kudu*), the wilde-beeste (Connochætes) carry about in the fluid portion of their blood, without themselves suffering any harm, certain protozoan trypanosomes which are fatal when borne by flies to domesticated horses (Equidæ), dogs (Canidæ), and cattle (Bovidæ).

Thus, causes favorable either to the genesis of these disease organisms or to the acquirement of immunity, or to the propagation and distribution of flies and ticks become matters of prime interest in relation to extinction.

Tse-tse Fly Disease of Domesticated Equidæ and Bovidæ.—The nagana or tse-tse fly disease of Africa is caused by *Trypanosoma brucei* (Plimmer and Bradford); the carrier is the tse-tse fly (*Glossina morsitans*). Together this trypanosome and its host the fly render thousands of square miles of Africa uninhabitable and no horses, dogs, or cattle can venture even for a day into the 'fly country.' After all the non-immune animals of the country have been killed off and thus no longer exist as sources of infection, the tse-tse fly spreads abroad out of the 'fly country' still giving rise to the disease. This strange fact led to the discovery of the fact noted above that many of the immune wild ruminants carry the same trypanosome (*T. brucei*) in small numbers in their blood and thus act as continuous reservoirs of the infection; it is from them that the fly obtains fresh supplies of the infectious parasite. A similar parasite also lives in the blood of healthy rats.[1]

Ticks, the Rapid Spreaders of Disease among Domestic Ruminants.—The *Piroplasma parvum* is a protozoan which, unlike the trypanosome, invades the blood corpuscle; it is malignant with cattle along the greater part of the east coast of Africa causing what is known as 'east-coast fever'. The infection is usually transmitted by ticks (most frequently by the brown tick, *Rhipicephalus appendiculatus*, also by *R. simus*). Migrating or treking cattle may carry the ticks many miles a day, and thus spread the

[1] Analogous to this is the 'sleeping-sickness' disease affecting man, which has spread very rapidly from west to east Africa, carried by a fly, *Glossina palpalis*, claiming hundreds of thousands of victims.

disease rapidly over a wide area of country. The larva creeps on an infected animal, sucks some of its blood, drops off, lies among the roots of the grass, and passes its first moult becoming a nympha, then an imago, in either of which latter stages it may infect a healthy animal by creeping from the grass. The tick is very hardy and may survive with its infection for a year, but after a year or fifteen months the infected ticks are all dead and healthy cattle may enter the field without risk.

Wide Geographical Distribution.—*Piroplasma bigeminum* similarly causes the 'Texas' or 'red-water fever' of our Southern States; it is conveyed by a tick. The germs are latent and the blood of an animal which has recovered from Texas fever remains infective; thus apparently healthy cattle may infect imported susceptible cattle. Such latency has an important bearing upon the theory of natural extinction as caused by similar germs. The geographical distribution of this species of Piroplasma is very wide; first discovered in North America, it is now epidemic throughout most of South Africa. Although acquiring immunity, it is the domesticated native Bovidæ which act as reservoirs of the disease in contrast to the tse-tse fly disease in which the wild Bovidæ act as reservoirs. The further fact that the native cattle may become immune has an important theoretical bearing on the natural origin of immunity to the tse-tse fly disease on the part of the wild Bovidæ and wild Equidæ.

Ticks among Equidæ.—The biliary fever of domesticated Equidæ (horses, mules, donkeys) is conveyed by a corpuscle parasite, *Piroplasma equi*, which is spread by the red tick, *Rhipicephalus evartsi*, the infection taken in the nymphal and transferred in the adult stage. As in the case of Texas fever in cattle, so the native South African horses become immune to the disease and are said to be "salted," but equines which have recovered from the disease continue to act as reservoirs and remain as sources of infection throughout their lives. The same is true among the Carnivora of the *Piroplasma canis*, spread by the dog tick (*Hæmophysalis leachii*). The blood of recovered animals remains infective.

Extermination of Wild Ruminants.—The rinderpest or cattle disease has been the greatest destroyer of the wild African quad-

rupeds (compare Gregory, p. 266). It is fatal to the following forms: wild buffalo, Bos (Bubalus), the kudu (*Strepsiceros kudu*), the sable antelope (*Hippotragus niger*), the gnu (*Connochætes albojubatus* and *C. taurina*), also in the Philippines to the carabao (*Bos* (*Bubalus*) *kerabau*). It is fatal to from 90 to 100% of domesticated cattle. Unlike the diseases before considered: (1) the parasite causing rinderpest is undiscovered, (2) no *natural* immunity is known (methods of artificial immunity were discovered in 1893), (3) it is distinguished by the ease and rapidity with which it spreads in all countries, climates, and seasons, being carried even on the clothes and person of man. It therefore appears improbable (Bruce) that insects have anything to do with it. It may be due to a wind-borne bacterial organism.

This disease has been known from time immemorial in Europe and Central Asia. It is believed by some to have entered the Nile provinces of 1880, to have reached the Transvaal in 1896, and thus to have traveled the whole length of Africa in fifteen years. The spread in Africa has been largely through the wild ruminants.

By analogy we can imagine that a disease affecting the Pleistocene horses of North America may have traveled an equal distance, namely, from Texas to Patagonia, and destroyed all the South American Equidæ.

Local Distribution, Immunity. Horse Sickness.— A very important point for the naturalist is the fact that this disease is local in its distribution, prevailing in low countries and during wet seasons. The infection is not carried into the high country or during the dry season.[1] The parasite causing it is unknown, and is believed to be ultra-microscopic. It is believed to be carried in the blood because the 1,000th part of a single drop of blood injected under the skin of a healthy animal will cause death; some horses require a larger dose than others, indicating fluctuations in power of resistance or immunity. Unlike the foregoing diseases it is not

[1] The same climatic relation is true of the heart-water disease of cattle, goats, and sheep (Bovidæ), which is similar in distribution to the heart-water horse sickness and is carried by the bont-tick (*Amblyomma hebræum*), in that it dies out on the high veldt. Similarly again the *catarrhal fever of sheep* has a distribution in South Africa similar to that of horse sickness, and is probably carried by means of the same night-feeding insect.

endemic or permanent, but occurs in epidemics at intervals of from ten to twenty years. Its geographical distribution in South Africa is very wide: in Natal, Zululand, the greater part of Rhodesia, Bechuanaland, and Portuguese East Africa. Horses placed in fly-proof shelters even in exceedingly unhealthy places in no case incur the disease. The particular fly or insect carrier is still unknown. As in several of the foregoing diseases the infective power of the blood persists for years.

Natural Origin of Immunity.—For the student of extinction an important point to note, in connection with 'horse sickness,' is that while artificial immunity is thus far undiscovered, degrees of immunity and of natural immunity sometimes occur. Such variations in respect to immunity would in a state of Nature lead to the gradual selection of immune forms and the production of an immune race.

Summary as to Natural Extinction by Disease

To summarize these remarkable conclusions which we owe to the labors of Lewis, Koch, Theiler, Kilborne, Smith, Watkins, Pitchford, and many others, we undoubtedly have here an agency which must be seriously considered as an occasional if not a frequent cause of extinction of quadrupeds in the past. It will be noted (1) that in the case of the tse-tse fly disease the wild ruminants are the permanent though unharmed reservoirs of the infective protozoan; (2) that in Texas fever or red-water fever native immune Bovidæ are the permanent carriers of the disease organism; (3) that the 'rinderpest' appears to be in an early stage of its history as a disease in which neither domesticated nor wild Bovidæ have become naturally immune and all the Bovidæ act as reservoirs; (4) that in the east-coast fever the infective ticks survive for a year, while the permanent carriers of the infective organism are not discovered; (5) that in the biliary fever of domesticated horses, the recovered equines act as reservoirs; (6) similarly again that in 'horse sickness' of South Africa the infective power of the blood in a recovered animal persists for years.

Thus in these diseases we have all the conditions favorable for the wide distribution of insect-borne diseases which in past times

may have attacked various types of quadrupeds and resulted in extermination before natural immunity was acquired.

Living Environment. Competing and Hostile Mammalia

From the struggle with physical environment, with the living plant and insect environment, we now pass to the struggle with other mammals.

In the Tertiary of North America we witness:

(*a*) the rapid multiplication of certain local or native mammals;

(*b*) the repeated introduction by migration of new mammals, coming either singly or in waves;

(*c*) the slowly or rapidly sequent extinction of certain local animals.

Even considering the disastrous effects of glaciation and of desiccation this *competition*, because it has worked more widely and over longer periods of time, has been a tremendous agency of extinction.

Competition of Lower and Higher Types.— Of marsupials in competition with rodents in Australia Spencer[1] observes: "In the case of such smaller marsupials as, for example, species of *Sminthopsis* in which the number of young produced at a birth is from eight to ten and there are at least two broods in each year it is a matter of considerable surprise that they are not much more numerous than they are. The explanation is probably associated with the fact that there is a considerable length of time during which not only does the capture of the mother result in her destruction and in that of all the young ones [by birds of prey, for example], but that during this period she is severely handicapped by not being able to reach shelter rapidly. It may perhaps be objected to this that such an animal as a rabbit is handicapped by having to carry the young ones in utero for a much longer time than the marsupial does, but anyone who has seen the well-developed, pouch young ones of a marsupial will realize how much more cumbersome a burden they are than the uterine embryos of such an animal as a wild rabbit."

[1] Spencer, Baldwin. "Through Larapinta Land, A Narrative of the Horn Expedition to Central Australia." *Report of the Horn Expedition to Central Australia*, Sept. 1896, pp. 127–128.

As regards this principle, Wallace observes: "There is good reason to believe that the most effective agent in the extinction of species is the pressure of other species, whether as enemies or merely as competitors." Lyell[1] observes: "Extension of the range of one species alters that of others. In reference to the extinction of species it is important to bear in mind, that when any region is stocked with as great a variety of animals and plants as its productive powers will enable it to support, the addition of any new species to the *permanent* numerical increase of one previously established, must always be attended either by the local extermination or the numerical decrease of some other species."

Exception must be taken to the sweeping character of these statements: First, because the *eliminating action of a change in plant life* may have been the *real* cause of extinction in several cases where competition with other mammals is the *apparent* cause. For example the extinction of the Titanotheriidæ and Elotheriidæ may have been entirely due to changes in vegetation, rather than to competition with any other Herbivora.

Second, because the survival of the opossums (Didelphiidæ) in North America shows there may be striking exceptions to this principle.

The conclusion drawn from such exceptions is that of Darwin, namely, that the *keenest competitors are the animals of most nearly similar feeding habits*. There are, however, exceptions to Darwin's conclusion also, as the following instances prove.

Destruction of Food Supply by Smaller Browsing Animals.—The enormous changes in the quadruped life of the district encircling the eastern and southern sides of the Mediterranean are popularly attributed to secular changes of climate. Haan shows, however, that evidence for secular change of climate within the historic period is insufficient or actually negative. Parts of these regions were formerly inhabited by some of the larger quadrupeds which have since disappeared through the agency of man; it is equally true that the country could not support the life of these quadrupeds at the present time. There can be little doubt that the change in soil and vegetation has been indirectly caused by

[1] Lyell, C. *Principles of Geology*, vol. 2, 1872, p. 451.

deforestation of the hills and mountains, and this has largely been the result of the unrestricted browsing of large herds of sheep and goats, which has been going on since long before the Christian era. Even now the goats can be observed in certain parts of Palestine and Greece destroying the last of the forests and killing the seedling trees. Destruction of the forests led to the washing away of the soil and to the entire unfitness of the country for the support of any of the larger Herbivora.[1]

"The mastodon, for example," observes Morris[2] "needing great quantities of herbage for its food supply, might, in cases of severe drought, succumb to the food competition of the rabbit, or some still more insignificant creature, which, spreading in vast numbers over the country, devoured the sparse herbage and left its huge competitor to starve....Thus hosts of Herbivora may have frequently perished in consequence of an insect assault upon their food; and numerous Carnivora, thus deprived of their food, may have similarly perished."

Especially Intense on Islands.—This great change is paralleled by the influence of the goats on islands, as cited by Wallace[3] and Palmer.[4]

Palmer (*loc. cit.*) observes: "Sheep and goats when numerous are likely to cause widespread injury, particularly in forested regions. An instructive example of the damage done by goats is that on St. Helena, described by Wallace.[5] St. Helena is a mountainous island scarcely 50 square miles in extent, and its highest summits reach an elevation of 2,700 feet. At the time of its discovery, about the beginning of the sixteenth century, it is said to have been covered by a dense forest; to-day it is described as a comparatively barren rocky desert. This change has been largely brought about by goats first introduced by the Portuguese

[1] Osborn, H. F. "Preservation of the Wild Animals of North America." Address before the Boone and Crockett Club, Washington, Jan. 23, 1904, pp. 15–16.

[2] Morris, Charles. "The Extinction of Species." *Proc. Acad. Nat. Sci. Phila.*, 1895, p. 254.

[3] *Island Life*, 1880, pp. 280, 283–286.

[4] Palmer, T. S. "The Danger of Introducing Noxious Animals and Birds." *Yearbook U. S Dept. of Agric. for 1898*, p. 89.

[5] *Island Life*, 1880, pp. 283–286.

in 1513, and which multiplied so fast that in seventy-five years they existed by thousands. Browsing on the young trees and shrubs, they rapidly brought about the destruction of the vegetation which protected the steep slopes. With the disappearance of the undergrowth, began the washing of the soil by tropical rains and the destruction of the forests. In 1709 the governor reported that the timber was rapidly disappearing and that the goats should be destroyed if the forests were to be preserved. This advice was not heeded, and only a century later, in 1810, another governor reported the total destruction of the forests by the goats.

"The Santa Barbara Islands, and Santa Catalina off the coast of southern California, and the island of Guadalupe, off the Lower California coast, are utilized as ranges for goats. All these islands are dry and more or less covered with brush, but arborescent vegetation is comparatively scarce. The goats practically run wild, and already exist in considerable numbers. As yet the goats have not been on the islands long enough to cause any serious effects on the vegetation, and they may never bring about the ruin which has been wrought on St. Helena. But it is scarcely possible for the islands to be grazed by goats for an indefinite length of time without suffering serious damage."

Goats, however, do not always enjoy a monopoly of the food of islands as the case cited above from Linnæus proves.

Small Browsers in Relation to Carnivora.—In both instances cited above, unrestricted browsing and rapid multiplication of the goats have taken place under artificial conditions of protection of these animals from Carnivora. It is quite possible, however, that in certain regions under natural conditions the Carnivora themselves may have become extinct through epidemics or other causes, thus promoting the unrestricted multiplication of the smaller browsing animals so fatal to the vegetation and to the normal distribution of food supply of a country. The period during which these changes have taken place in the Orient is a comparatively short one as compared with the periods of geological time.

Application to the American Oligocene.—Thus we see that the introduction of new forms of *dissimilar feeders* may completely disturb the balance of Nature and entirely alter the character and amount of food supply or even of water supply and of com-

petition in any given region. Rabbits exert a great influence on the food supply of the marsupial Herbivora of Australia. This factor of the browsing competition of the smaller Herbivora on islands is one which, while by no means demonstrated, is a possible cause of extinction of the larger Herbivora in larger areas and is worth considering even in relation to the sudden disappearance of the Titanotheres. For example, the extreme multiplication of the Oreodonts (Oreodon, Agriochœrus) and horses (Mesohippus), small browsers which swarmed in herds in the Middle Oligocene period in the regions of South Dakota and Nebraska, may possibly have cut off part of the food supply of the Titanotheres.

Application to the Oligocene and Miocene of Europe.— Since the introduction and unchecked increase of small browsing animals may in course of a century or a number of centuries — a comparatively short period in geological time — effect a profound influence in a country upon the forests, since sheep and goats are forest destroyers especially under the artificial conditions where the increase of these animals is unchecked, and such browsers are especially destructive of the circumscribed flora of islands, we should consider the part the smaller browsing animals may have played during the Tertiary of Europe when so many parts were archipelagic.

Dwarfed Pliocene and Pleistocene Island Life.— In the islands of Malta, Cyprus, and Crete, as recently explored by Miss Bate,[1] we have fine examples of comparatively recent insulation.

It appears probable that Cyprus became an island first, because: (1) no submerged bank connects it with the mainland, and the 200-fathom line is reached within a short distance of the coast line; (2) the terrestrial fauna and avifauna include several distinct races peculiar to the island, a fact confirmed by Kobelt from his study of the recent Mollusca. The reduced existing Cyprus fauna contains a mingling of European and North African forms, and shows the effects of deforestation in historic times. The largest animal on the island is the moufflon (*Ovis ophion*) 25 inches high at the shoulders; yet this is the *smallest* of all the wild sheep, and is related to East Persian species.

[1] Bate, Dorothea M. A. "Pleistocene Mammalia in Crete." *Geol. Mag.*, n. s., dec. 5, vol. 2, pp. 193–202, May, 1905.

The affinity of Malta to Sicily is indicated by the occurrence of two species, *Hippopotamus pentlandi* and *Elephas mnaidriensis*, in the cavern deposits of both islands. The early separation of Cyprus is indicated by the fact that *E. cypriotes* and *H. minutus* are both more primitive than the Maltese-Sicilian species. Crete also includes antelope and deer in its Pleistocene fauna.

Pleistocene Extinct Fauna of the Mediterranean Islands

	Cyprus	Malta	Sicily	Sardinia
Proboscidea, pigmy elephants	*E. cypriotes*	*E. melitensis* *E. mnaidriensis*	*E. mnaidriensis*	*E. lamormoræ*
Artiodactyla, pigmy hippopotami	*H. minutus*	*H. pentlandi*	*H. pentlandi*	

The occurrence of these specifically different though apparently closely related races of small elephants and hippopotami in widely separated islands is an instance of independent development with some divergence from common ancestors.

Introduction of Carnivora

Striking examples of the introduction and competition of Carnivora in past and recent times are:

(1) The true Carnivora in competition with the Creodonta of Europe and North America, followed by the final extinction of the latter order in the Lower Oligocene.

(2) The true Carnivora in South America in the Middle Pliocene. At this time the Canidæ and two destructive types of Felidæ, the sabre-tooths (Machærodontinæ) and the true cats (Felinæ), suddenly appeared; they entered a faunal region which, subsequent to the extinction of the marsupial Carnivores (Thylacinidæ) in the Oligocene, had been entirely free from Carnivora.

(3) The dingo (*Canis dingo*), in the Australian mainland, followed by the extinction of the Tasmanian wolf (Thylacinus) and devil (Sarcophilus), animals which survive only in Tasmania.

(4) The mongoose (Herpestes) in various countries.

In each instance intelligence, ferocity, and facility in change of habit have played an important part. The Carnivora in relation

to the balance of Nature, the food supply, the *young* of the Herbivora is our special inquiry.

Smaller Carnivora and the Balance of Nature.— T. S. Palmer[1] has given a striking summary of the influence of the mongoose:

"The common mongoose of India (*Herpestes mungo* or *H. griseus*).... is a well known destroyer of rats, lizards, and snakes, and was introduced into Jamaica....for the purpose of ridding cane fields of rats....Various remedies were tried, but apparently with little success, until in February, 1872....nine individuals of the mongoose, four males and five females, from India, were introduced. These animals increased with remarkable rapidity, and soon spread to all parts of the island, even to the tops of the highest mountains. A decrease in the number of rats was soon noticeable....The mongoose increased, and as the rats diminished, its omnivorous habits became more and more apparent. It destroyed young pigs, kids, lambs, kittens, puppies, the native 'coney' or capromys poultry, game, birds which nested on or near the ground, eggs, snakes, ground lizards, frogs, turtles' eggs, and land crabs. It was also known to eat ripe bananas, pineapples, young corn, avocado pears, sweet potatoes, cocoanuts, and other fruits. Toward the close of the second decade the mongoose, originally considered very beneficial, came to be regarded as the greatest pest ever introduced into the island. Poultry and domesticated animals suffered from its depredations, and the short-tailed capromys (*Capromys brachyurus*), which was formerly numerous became almost extinct except in some of the mountainous districts. The ground dove (*Columbigallina passerina*) and the quail dove (*Geotrygon montana*) became rare, and the introduced bobwhite, or quail, was almost exterminated. The peculiar Jamaica petrel (*Æstrelata caribbæa*), which nested in the mountains of the island, likewise became almost exterminated. Snakes, represented by at least five species, all harmless, and lizards, including about twenty species, were greatly diminished in numbers. The same thing was true of the land and fresh-water tortoises and the marine turtle (*Chelone viridis*), which formerly laid its eggs in

[1] Palmer, T. S. "The Danger of Introducing Noxious Animals and Birds." *Yearbook U. S. Dept. of Agric. for 1898*, pp. 93, 94.

abundance in the loose sand on the north coast. The destruction of insectivorous birds, snakes, and lizards was followed by an increase in several injurious insects, particularly ticks, which became a serious pest, and a Coccid moth, the larvæ of which bore into the pimento trees."

Carnivorous Animals Directly Hostile.— The question as to how far the mammals of prey have caused the extinction at various times of various forms of quadruped life is widely disputed. Morris[1] observes: "So far as existing evidence goes, then, it seems probable that hostile aggression, while it may have occasionally been an indirect, has rarely been the direct cause of the extinction of species." The similar opinion expressed to the writer by Dr. D. G. Elliot that no wild animal causes the extinction of another wild animal is probably true (1) of undiminished herds, (2) of cases where carnivores and quadrupeds have evolved together and, as in the case of the modern battleship, modes of defence have evolved simultaneously with modes of attack.

In this connection, however, we must consider the Carnivora as one of the causes of *final extinction* of diminished groups of animals which are struggling to maintain themselves against adverse conditions of (*a*) physical environment, droughts, or cold, (*b*) changing food supply, (*c*) competition with other quadrupeds, (*d*) epidemics.

The above opinions (of Morris and Elliot), therefore, do not hold good (3) of diminished herds, which are unable adequately to defend their young, or (4) of cases where newly introduced Carnivora find quadrupeds unprovided with adequate means of defence, as in the South American invasion from North America in the upper Pliocene.

INTERNAL CAUSES OF EXTINCTION

Environment and life (including heredity and ontogeny) are *always* reciprocal. Having considered the causes of extinction which originate in the environment let us pass to those which originate in a lack of internal adaptation and adaptability.

[1] "The Extinction of Species." *Proc. Acad. Nat. Sci. Phila.*, June, 1895, pp. 253–263.

Important Differences Between the Effects of Internal and External Causes

Summarizing the external causes we observe:

(1) That in large part they originate with cosmic changes, or with changes in the earth itself, in the elevation or depression, extension or contraction of the land and water areas. From these result progressive heat or cold under both moist and dry conditions, progressive moisture and desiccation, consequent changes of soil, vegetation, forestation, water supply. Also the introduction of new food competitors or enemies, of new insect pests and new diseases.

(2) Under these changed conditions we observe that the extinction of species and genera has repeatedly occurred on a very large scale. Secular desiccation in different periods of the Tertiary, but chiefly toward the late Pliocene, was quite as fatal as the Glacial Period.

(3) A distinctive feature of such extinction, *originating in external causes*, is that it often affects the fit and unfit alike, the adapted and inadapted; it often destroys rather than improves a fauna. This was certainly the case with the glacial extinction in North America and Europe.

(4) On the contrary, the extinction, *originating in internal causes, i. e., in relative internal fitness or unfitness*, often improves a fauna by eliminating the least adapted members.

(5) A further distinction is that external causes have usually acted locally or on certain parts of the earth's surface, leaving a part of the fauna to survive elsewhere. The elimination of the Equidæ and Proboscidia in North and South America, for example, did not hinder their survival in the Old World.

(6) Internal causes, relative inadaptation or unfitness, have, on the contrary, acted simultaneously all over the world, for example, in the elimination of the great orders of Creodonta, Amblypoda, and Condylarthra during the Eocene period.

Survival or Extinction Value of Organs

Paleontology affords positive evidence that structural or functional inadaptations have been primary causes of extinction at all times but chiefly during periods of external change.

(1) Since the publication of *The Origin of Species* naturalists have disagreed as to one of Darwin's main propositions, namely, that the struggle for existence is so intense that variations adaptive or inadaptive, no matter how slight, will tend respectively toward survival or elimination. This raises the question of the modes of evolution, of *character or organ building*, in mammals, which is treated elsewhere.

(2) Whatever may be true as to the above feature of the selection theory, there is a general consensus of opinion that *animals which present the highest adaptive combination of favorable characters, of fully formed organs, and the highest adaptability or capacity of favorable change of habit or structure, will tend to survive.*

(3) Similarly there is a consensus, from certain repeatedly observed facts in paleontology that in *varietal*, *specific*, *generic*, *family selection*, not only adaptive or inadaptive *combinations* of characters but also *single fully formed organs*, such as the brain, the limbs, and the teeth, have in course of time been the causes of selection or extinction, partly in connection with changes of environment, partly because inherently adaptive or inadaptive.

(4) Thus we make the generalization that in certain cases extreme bulk, extreme specialization, the development of certain dominant characters, have led to extinction; that large-brained have replaced small-brained types; that certain types of teeth or certain types of limb and foot structure have simultaneously over large parts of the world been found wanting and thus proved fatal to their possessors.

These are the general lines of thought which have been followed by many authors since Darwin first directed our attention to this subject. It is necessary, however, to look into these causes somewhat more critically since many of them have been assumed without proof.

Inadaptive Foot and Molar-Tooth Structure.— Waldemar Kowalevsky, the Russian paleontologist, was one of the pioneers in this line of reasoning. He observed in his great monograph [1]

[1] "Monograph der Gattung Anthracotherium Cuv. und Versuch einer natürlichen Classification der fossilen Hufthiere." *Palæontographica*, n. s., vol. 2, 3. (XXII.)

(1873, p. 152) the *extinction of all Artiodactyla* with an inadaptive foot structure and inadaptive grinding teeth as follows: *Upper Eocene*, Xiphodon, Anoplotherium, Diplopus; *Oligocene*, Hyopotamus, Anthracotherium, Entelodon. He pointed out that the inadaptation of the foot in these animals consisted of a mechanical defect in the manus (3d metacarpal not spreading above to articulate with the trapezium as in the 'adaptive' manus of the pig and hippopotamus, see Taf. 7), and that the inadaptation in the grinders consisted of the persistent short or brachyodont crowns, bunoselenodont and bunodont, composed of partially rounded cones. These feet being mechanically weak in the function of the carpals and metacarpals were incapable of the elongation into cannon bones — a cursorial or speed adaptation which saved the lives of the adaptively reduced Artiodactyls. These short teeth were by his theory not adapted to a supposed change of vegetation from softer herbage to harder Gramineæ. His paleozoölogical supposition that such a change of food occurred was independently confirmed by the paleobotanists Saporta and Marion. His conclusion as to extinction (which was very original at the time) has since been abundantly confirmed by subsequent observations of the extinction of all forms of quadrupeds with these inadaptive types of short-crowned grinders both in North America and in India.

This generalization is noteworthy also as bearing upon the extinction of the Titanotheres (Oligocene) and Chalicotheres (Upper Miocene) types, both of which possess short-crowned bunoselenodont molars.

Inadaptation of the Titanothere Grinding Teeth.— It has since been recognized by every author who has written upon these animals that the relatively short crowns of the so called bunoselenodont or combined cone-and-crescent pattern of grinding teeth, were adapted to browsing on coarse and soft rather than fine and hard kinds of food. Thus Lucas [1] observes: "....it is easy to see from a glance at their large, simple teeth that these beasts [Titanotheres] needed an ample provision of coarse vegetation and as they seem never to have spread far beyond their birthplace,

[1] *Animals of the Past.* 8vo, New York, 1901, p. 222.

climatic change modifying even a comparatively limited area would suffice to sweep them out of existence."

In the summary of the tooth characters of the Titanotheres we have shown how Nature was apparently making an effort to develop a long or hypsodont crown by the elongation of the ectoloph on the outer side of the superior grinding teeth, and secondly how this effort was apparently futile because of the separate rise or development of the inner or cone side of the tooth and the absence of a transverse crest. Such a tooth is half hypsodont and half brachyodont. It does not favor longevity because it is soon worn off.

A *cul de sac* in evolution is an avenue from which there is no escape. This was reached in the teeth of the Titanotheres not, as in many other animals by a great sacrifice of numbers in the specialization of the teeth, but by a sacrifice of *parts*; the intermediate tubercles were lost and the internal tubercles were isolated. It is noteworthy that every animal experimenting with teeth of this kind (Anoplotheriidæ, Anthracotheriidæ, Chalicotheriidæ) became extinct; there was no further mechanical progress or perfection possible, hence the *cul de sac*. At this point an animal is at the mercy either of its competitors or of a change of vegetation. We conclude from the extinction of the large-toothed *Titanotherium ingens* that it was not the size of the teeth but the mechanical pattern which was inadaptive.

While it appears that the Titanotheres with their immense bodies were poorly equipped for the competition for food, and would have been seriously affected by any change of climate which greatly altered the general vegetation, especially if it resulted in an increase of grasses and a decrease of the softer plants, we must record the fact that the Elotheres, *with still less effective teeth*, passed through exactly such a crisis (if it occurred), that soon afterward they began a very rapid increase in size, and that they survived to a much later geological period (Lower Miocene).

Regarding the influence of the teeth as chief factors in extermination there is the strong collateral evidence for Kowalevsky's theory as described above, that since all bunoselenodont quadrupeds whether belonging to the Artiodactyla or Perissodactyla, disappeared either during the Oligocene or early Miocene period

in all parts of the world, the possession of this type of tooth was the primary cause of extinction.

Of all the possible causes of extinction of the Titanotheres this seems to be the one which has the strongest collateral support. Yet the suddenness of Titanothere extinction seems to require the existence of contributory causes.

Relation of Molar-Tooth Structure to Longevity and Reproductive Power.— There is obviously a direct correlation between longevity and fertility with *hypsodontism*, or the elongation of the crowns of the grinding teeth, which enables an animal to live a great many years. Elephants, according to Darwin's calculation, although slow-breeding animals, with the aid of their extremely long-crowned teeth live 90 years and produce at least three pair of young. Horses with their long-crowned teeth, living to the age of twenty-five years and foaling every year would produce twenty-two young.

In contrast such a titanothere type as Palæosyops, with its short-crowned teeth, would live a comparatively short period and produce comparatively few young. In the long run this relation of longevity to reproduction would tend to replace the races with short-crowned teeth by those with long-crowned teeth.

Theoretically this law might be one of the means of explaining the early dying out of the short-crowned, broad-skulled genus Palæosyops, if it were not for the contradictory fact that the short-crowned Manteoceras survived and that the long-crowned Telmatherium became extinct.

Feet and Limbs.— Like the teeth, the feet of the Titanotheres were practically stationary in development. Just as the Oligocene tooth is an enlarged duplicate of the Eocene tooth, so the Oligocene titanothere foot is an enlarged duplicate of the Eocene foot.

Since the remains of these animals are found chiefly in coarse river channel deposits, there is no geological evidence that these animals suffered from a scarcity of water. The floods, however, may have been periodic with intervals of drought and it may be imagined that under changing conditions of plant life the titanothere feet and limbs were not adapted to long excursions for food enforced during the annual dryer periods, as compared with other quadrupeds. But the Titanotheres were certainly not far inferior

travelers to the contemporary rhinoceroses, and were equal to the modern elephant type. This therefore may be considered as a contributory cause rather than as one of the chief causes of titanothere extinction.

THE INADAPTATION OF LARGE SIZE

There is a widespread belief, which is not borne out by the facts, that bulky animals have tended to disappear first.

Thus Owen, although as late as 1877[1] disposed to attribute the extinction of the large mammals of Australia to the agency of man, advanced the theory[2] of the disadvantages of bulky size under changed conditions. "In proportion to the bulk of a species is the difficulty of the contest which, as a living organized whole, the individual of such species has to maintain against the surrounding agencies that are ever tending to dissolve the vital bond, and subjugate the living matter to the ordinary chemical and physical forces. Any changes, therefore, in such external conditions as a species may have been originally adapted to exist in, will militate against that existence in a degree proportionate, perhaps in a geometrical ratio, to the bulk of the species. If a dry season be gradually prolonged, the large Mammal will suffer from the drought sooner than the small one; if any alteration of climate affect the quantity of vegetable food, the bulky Herbivore will first feel the effects of stinted nourishment.....The actual presence, therefore, of small species of animals in countries where larger species of the same natural families formerly existed, is not the consequence of any gradual diminution of the size of such species, but is the result of circumstances which may be illustrated by the fable of the 'oak and the reed'; the smaller and feebler animals have bent, as it were, and accommodated themselves to changes which have destroyed the larger species."

Morris[3] observes: "....One tendency, which has particularly

[1] *Researches on the Fossil Remains of the Extinct Mammals of Australia.* 4to, London, 1877, pp. ix, x.

[2] *Trans. Zool. Soc. London*, vol. 4, 1850, p. 27.

[3] Morris, Charles. "The Extinction of Species." *Proc. Acad. Nat. Sci. Phila.*, 1895, p. 254.

manifested itself in herbivorous animals, has frequently led directly to their destruction. This is the tendency to increase in size through the double influence of abundance of food and little waste of tissue through exertion. In the sluggish grass-eaters, dwelling on plains covered with rich herbage, or leaf and twig eaters in tropical forests, the nutritive agencies are in excess of those of waste, and these animals seem always to have tended to an increase in size, until those of least exertion and greatest powers of obtaining food became enormous in dimensions. An example of the same kind among the Carnivora is the Greenland whale, which, while feeding on minute forms, obtains them in enormous quantities with little muscular exertion, and has in consequence become of extraordinary dimensions. . . ."

Bulk not Intrinsically Fatal.—(1) The extinction of a large quadruped attracts more attention but we recall the fact (*a*) that the small Condylarthra became extinct before the large Amblypoda, (*b*) that many families of relatively small Artiodactyla and Perissodactyla became extinct at the same period as the very large Titanotheres; (*c*) that the relatively small Mylodon disappeared as early as the large Megatherium; (*d*) that the extinction of the mammoth in the northern hemisphere during or after the glacial epoch attracts attention because of the animal's large size, but as shown, many other quadrupeds vastly inferior in size disappeared at the same time.

(2) The survival of animals which have been constantly increasing in size from the Eocene to the present time may be cited as proof that bulk is not a cause of elimination *per se*. The wild horses, rhinoceroses, many ruminants, bears, and probably the whales have now attained the maximum size. The African elephant is practically as large as any of the extinct species. Both the elephant and the white rhinoceros (which would have survived in large numbers but for the purely accidental interference with the order of Nature by man) are perfectly adapted in these two respects.

(3) Bulk is fatal under certain changes of environment where not correlated with an adequate feeding mechanism, with adequate defensive powers, adequate fertility, and adequate defense and care of the young.

But the *absence of these powers is almost equally fatal to small animals.*

Bulk must therefore be considered in relation to (1) disadvantage of the large amount of food required by a large animal, which is offset by the advantage that many large animals can travel long distances; (2) diminished birth rate, which is a characteristic of large animals, is a point to be noticed; as a rule, the larger the animals, the fewer the young, and the less able a species would be quickly to regain numerical strength after some widespread diminution in number; (3) by the fact that the diminished birth-rate is offset by longevity and power to protect young from enemies. "The elephant," observes Darwin, "is reckoned to be the slowest breeder of all known animals, and I have taken some pains to estimate its probable minimum rate of natural increase: it will be under the mark to assume that it breeds when thirty years old, and goes on breeding till ninety years old, bringing forth three pair of young in this interval; if this be so, at the end of the fifth century there would be alive fifteen million elephants, descended from the first pair."[1]

Application to the Titanotheres.—The bulk of the Titanotheres, which exceeded that of any other land quadrupeds, excepting only the more modern elephants, may have been a serious drawback under changing conditions of vegetation; but as noted above the extinction of the huge Titanotheres was no more sudden or mysterious than that of the slender Hyracodontidæ and Lophiodontidæ, or of the Amynodontidæ—all contemporaries of the Titanotheriidæ and vastly inferior in size.

It is important to note that whereas in the elephant the diminished birth rate is offset by longevity this *was not the case* in the Titanotheres which with their very short-crowned teeth were relatively short-lived animals.

Bulk, Slow Breeding, and Variation.—The following argument by Wallace receives no support from paleontology. "There is, however, another cause for the extinction of large rather than small animals whenever an important change of conditions occurs, which has been suggested to me by a correspondent,[2] but which has not,

[1] Darwin, C. *Origin of Species*, p. 63, ed. of 1860.
[2] Mr. John Hickman of Desborough.

I believe, been adduced by Mr. Darwin or by any other writer on the subject. It is dependent on the fact, that large animals as compared with small ones are almost invariably slow breeders, and as they also necessarily exist in much smaller numbers in a given area, they offer far less materials for favourable variations than do smaller animals. In such an extreme case as that of the rabbit and elephant, the young born each year in the world are probably as some millions to one; and it is very easily conceivable that in a thousand years the former might, under pressure of rapidly changing conditions, become modified into a distinct species, while the latter, not offering enough favourable variations to effect a suitable adaptation, would become extinct."[1]

Mr. C. W. Andrews[2] has recently (1903) revived this argument that the lengthening of the time taken to attain sexual maturity may affect the rate of evolution, and under changed conditions where a rapid rate of evolution is essential may cause extinction.

"....In many Ungulates this increased longevity is indicated by various modifications of the teeth, tending to give them a longer period of wear: generally this end is attained by the increasing hypselodonty of the cheek-teeth. A necessary consequence of the longer individual life will be that in a given period fewer generations will succeed one another, and the rate of evolution of the stock will therefore be lowered in the same proportion. If now the conditions of life undergo change, the question whether a given group of animals will survive or become extinct will depend upon whether it can undergo sufficiently rapid variation to enable it to avoid getting so far out of harmony with its surroundings that further existence becomes impossible. It seems to follow then that the smaller animals, in which the generations succeed one another rapidly, will have a better chance of surviving than the larger and more slowly breeding forms, which at the same time will be still further handicapped if, as is usually the case, they are more highly specialized than the smaller forms, and therefore have a more restricted range of possible variation."

[1] Wallace, A. R. *Geographical Distribution of Animals*, vol. 1, pp. 158–159.

[2] Andrews, C. W. "Some Suggestions on Extinction." *Geol. Mag.*, dec. 4. vol. 10, no. 463, January, 1903, p. 2.

As against these purely hypothetical considerations paleontology shows that during Pliocene and Pleistocene times the slow-breeding Proboscidia evolved quite as rapidly, if not more rapidly, than the rapid-breeding Rodentia.

THE INADAPTATION OF EXTREME SPECIALIZATION

Extreme Specialization.—Specializations among the quadrupeds take many forms: the *loss of parts* which under changing conditions might be useful. In the case of the Titanotheres the diminished size of the cropping teeth, which are either degenerate or wanting, is an instance. The animals while capable of browsing were *incapable of grazing,* so far as we can infer from the general presence of well adapted paired or single cropping teeth in the surviving ruminants and horses. It may be said that the Titanotheres had lost all cropping power through the degeneration, simplification, or absence of the incisor teeth.

Survival of the Unspecialized.—This is a general but not universal principle. Cope observes:

"Agassiz and Dana pointed out this fact in taxonomy, and I expressed it as an evolutionary law under the name of the 'Doctrine of the Unspecialized.' This describes the fact that the highly developed, or specialized types of one geologic period have not been the parents of the types of succeeding periods, but that the descent has been derived from the less specialized of preceding ages. No better example of this law can be found than man himself, who preserves in his general structure the type that was prevalent during the Eocene period, adding thereto his superior brain-structure.

"The validity of this law is due to the fact that the specialized types of all periods have been generally incapable of adaptation to the changed conditions which characterized the advent of new periods. Changes of climate and food consequent on disturbances of the earth's crust have rendered existence impossible to many plants and animals, and have rendered life precarious to others. Such changes have been often especially severe in their effects on species of large size, which required food in large quantities. The

results have been degeneracy or extinction. On the other hand plants and animals of unspecialized habits have survived."[1]

Dominant Characters.— Characters which have reached an extreme stage so as to demand a larger share of the sum total of bodily nutrition than their general or apparent utility justifies may be known as *dominant organs.* They appear to violate the law of economy of growth, or the maximum combination of favorable characters by the subservience of each part to the whole.

The great horns of the Titanotheres, the tooth of the narwhal, the tusks of the Babirussa, the horns of the Irish deer, Megaceros, the tusks of the mammoths, *E. primigenius*, *E. columbi*, and *E. imperator*, are cases in point. The tusks of the elephants, however, serve a variety of useful purposes.

Overdevelopment of such organs has long been considered among the possible causes of extinction. The overdevelopment itself has recently been explained by F. B. Loomis[2] as follows:

"The above are selected examples in which a feature once useful has been developed beyond its maximum utility. Many others equally striking might be cited, the explanation of all of which is extremely difficult unless such a factor as momentum is called in. In the light of this factor, however, a logical and apparent cause is found. Momentum also explains why a character that originated in accordance with the environment develops so rapidly, and why, when an animal had reached adjustment to its surroundings, it still goes on beyond a perfect adjustment. It may be laid down as a rule then that *a variation started along any line tends to carry that line of development to its ultimate, being driven by momentum.* If the feature is detrimental the group dies out; if, however, it is merely a minor feature it makes a handicap. A line of development may be stopped and its momentum overcome but the tendency is to keep right on."

Selection of Useless Dominant Organs.— Another explanation may be offered for certain male dominant characters, namely, that by sexual selection or competition between the males for females, characters are precociously or overdeveloped, which are

[1] Cope, E. D. *Primary Factors of Organic Evolution*, 1896, p. 173.

[2] Loomis, F. B. "Momentum in Variation." *Amer. Nat.*, vol. 39, 1905, p. 843.

of little use in general selection and competition with other animals. Thus in the case of horns, of tusks, and of canines, by favoring the males in which they are most strongly developed they cause an *incidence* of selection on characters which are useful in sexual selection only.

Extreme specialization in several members of the titanothere family took the form of dominance of the horns. As we have seen, the horns first appeared alike in both sexes as rudiments or small horns but gradually they became male characters, and were undoubtedly of advantage to the males in their sexual combats for the possession of the females. Thus a constant selection of the individuals with the largest horns may have been in process. This incidence or main emphasis of natural selection on characters which were useless for feeding purposes may have been the cause of the non-evolution of the teeth.

The force of this generalization is, however, weakened by the fact that in other Titanotheres, such as the genera Titanotherium and Megacerops, the horns were relatively small, yet these animals became extinct at the same time as the large-horned genera, Brontotherium and Symborodon.

PSYCHIC OR CEREBRAL INADAPTATION

Brain.— Under temporary or prolonged changed conditions of life, intelligence and instinct are matters of first importance in relation to quickness, alertness, adaptability to new conditions. Animals differ enormously in this regard. On our western plains horses by their resourcefulness save their lives where cattle perish.

The paleontologist knows nothing of these psychic qualities, he can only judge the powers of an extinct animal by examining the intra-cranial cast which often reproduces the external form of the brain with great fidelity. The chief measure of the capacity of extinct animals is indicated by:

(1) absolute size and weight of the brain;
(2) development of the convolutions;
(3) proportionate size of the frontal lobes of the cerebrum;
(4) ratio of brain weight to body weight.

Lortet was the first to establish the law of the progressive cerebral development of the Tertiary mammals.

In 1884 Marsh briefly considered the brain question in relation to the extinction of the Titanotheres or Brontotheriidæ. He observes (p. 190): "The small brain, highly specialized characters, and huge bulk, rendered them incapable of adapting themselves to new conditions, and a change of surroundings brought extinction." Again (p. 190): "The Dinocerata, with their very diminutive brain, fixed characters, and massive frames, flourished as long as the conditions were especially favorable, but with the first geological change, they perished, and left no descendants." In discussing the brain, especially after referring to the general law of brain growth (*i. e.*, evolution) during the Tertiary period, he states:

"To this general law of brain growth two additions may now be made, which briefly stated are as follows: (1.) The brain of a mammal belonging to a vigorous race, fitted for a long survival, is larger than the average brain, of that period, in the same group. (2.) The brain of a mammal of a declining race is smaller than the average of its contemporaries of the same group." [1]

As above noted the chief advantages of brain capacity are undoubtedly in relation to adaptability of habit, resourcefulness in times of exposure, alertness in avoiding new dangers to which the young may be exposed, enterprise in seeking new habitat, qualities which should be more fully considered under the law of adaptive variation and the evolution principle of organic selection.

Arrested Variation

Brocchi on the Dying Out of Species.— An Italian geologist, Brocchi,[2] the author in 1814 of an able work on the fossil shells of the sub-Apennine hills, endeavored to imagine some regular and constant law by which species might be made to disappear from the earth gradually and in succession. The death, he suggested of a species might depend, like that of individuals, on certain peculiarities of constitution conferred upon them at their birth; and as the longevity of the one depends on a certain force of vitality,

[1] Marsh, O. C. "Dinocerata, an Extinct Order of Gigantic Mammals." *Mon. U. S. Geol. Surv.*, vol. 10, Washington, 1884, p. 59.

[2] Brocchi. *Conch. foss. subap.*, vol. 1, 1814.

which, after a period, grows weaker and weaker, so the duration of the other may be governed by the quantity of prolific power bestowed upon the species which, after a season, may decline in energy, so that the fecundity and multiplication of individuals may be gradually lessened from century to century, "until that fatal term arrives when the embryo, incapable of extending and developing itself, abandons, almost at the instant of its formation, the slender principle of life by which it was scarcely animated, and so all dies with it."[1] Lyell opposed this doctrine on the ground that there is seldom evidence of physiological deterioration in the last representatives of a species.

This idea of *self extinction*, as applied to a theoretical arrest of variation was expressed in another form by Darwin and Wallace and has been recently revived.

The Limiting of Variation.—The theoretical importance assigned to the *limiting of variation* (independently of environment) as a cause of extinction depends partly upon one's theoretical opinions as to the modes of evolution. In the citations made above from Darwin (p. 852), Wallace (p. 852) and Andrews (p. 853) the theoretical view is taken that since (1) a limitation or cessation of fortuitous variation would cut off material for improvement through selection, (2) a fixed or non-adaptable type would arise and (3) extinction would follow.

Similarly Mr. C. B. Crampton (as cited by C. W. Andrews)[2] suggests an inherent cause of extinction as follows: " . . . . In a recent paper by Mr. C. B. Crampton (*Proc. Roy. Phys. Soc. Edinburgh*, vol. xiv, p. 461) a possible inherent cause of extinction is suggested. It is impossible to do justice to this interesting paper in a short note, but the gist of the argument seems to be as follows:—In the original unicellular organism the possibilities of variation are almost infinite, but as soon as evolution along any line begins, these possibilities are restricted, and become more and more so the more highly specialized the animal is; in short, the potential variation of an organism becomes less and less as specialization advances. Furthermore, under the influence of

[1] Lyell, Charles. *Principles of Geology*, vol. 2, 11th ed., 1892, p. 270.

[2] Andrews, C. W. "Some Suggestions on Extinction." *Geol. Mag.*, dec. 4, vol. 10, no. 463, p. 1, January, 1903.

natural selection, in each generation the individuals which tend to vary in the same direction will survive, while at the same time, as already pointed out, their capacity for variation becomes more and more restricted. The consequence of this will be that the more highly specialized any stock becomes, the more the individuals composing it will come to resemble one another, until at length the same results as arise from close inter-breeding, *viz.*, weakening of the stock, and, finally, extinction, may follow."

This is purely a question of evidence and all the evidence we can muster is negative. Invertebrate paleontologists cite cases of extinction being preceded by an efflorescence of new structures.

Among the Vertebrata no evidence has been adduced of extinction being preceded by an arrest of variation, *i. e.*, of evolution. On the contrary extinction often occurs at the high tide of change and not after a prolonged period of stability.

Conclusion

The chief induction which can be made from this extensive survey of the causes of extinction seems to be this: *following the diminution in number which may arise from a chief or original cause, various other causes conspire or are cumulative in effect.* From weakening its hold upon life at one point an animal is endangered at many other points.

THE ALPINE FLORA OF COLORADO

T. D. A. COCKERELL

In 1881 (*Bull. U. S. Geol. and Geogr. Surv. Terr.*, vol. 6, no. 1) Gray and Hooker gave a list of the alpine plants of the Rocky Mountains: 184 species, of which 102 extended to the arctic or subarctic regions. Since that time, our knowledge has greatly increased, but the records have been scattered in many publications, and no summary has been available. The appearance of a new Flora of Colorado, written by Dr. P. A. Rydberg and issued by the Colorado Agricultural Experiment Station (*Bulletin 100*, 1906) makes it possible to gather together the known facts, so far as they relate to that State, and derive from them some general conclusions.

It is not pretended, of course, that the information given by Rydberg is complete; and it must doubtless be admitted that some of the recently described species probably do not deserve that rank; but allowing for these and other elements of doubt and difficulty, we may still recognize many broad facts which are not likely to be overthrown. With regard to the details, each statement may be regarded as a challenge to Colorado botanists, to refute it if they can, and in this way even error may be made the cause of progress. The Arctic-Alpine Zone begins at timber line, or the upper limit of trees. This may be roughly placed at an altitude of 12,500 feet, but it differs according to the character of the exposure as well as the latitude, and may actually descend considerably lower. In order to omit nothing, I listed all the plants given by Rydberg as growing at 12,000 feet or above: 386 species. Of these, 202 are not recorded as going above 12,500 feet, and may therefore not pass beyond the Hudsonian Zone; 92 of the 386 descend to below 8000 feet, and of these, 62 do not go above 12,500 feet.

Old World Species

Forty-eight species (probably more!) extend to the Old World,

most of them being circumpolar, but a few only reaching eastern Asia. I have divided these into four groups:—

(1) Going above 12,500 feet, and not below 11,000 (10 species):—

Carex incurva Lightf.
C. atrata L.
C. pyrenaica Wahl.
C. rupestris All.
C. microglochin Wahl.
Papaver radicatum Rottb.
Saxifraga cernua L.
Dryas octopetala L.
Dasystephana romanzovii (Ledeb.)
Sagina nivalis Fries.[1]

(2) Going above 12,500, but also below 11,000 feet (16 species):—

Filix fragilis (L.).
Trisetum subspicatum (L.).
Poa alpina L.
Elyna bellardi (All.).
Carex nigricans C. A. Mey. (to Asia).
Juncoides spicatum (L.).
Lloydia serotina (L.).
Oxyria digyna (L.).
Silene acaulis L.
Draba aurea Wahl.
Muscaria adscendens (L.).
Leptasea flagellaris (Willd.).
Potentilla nivea L.
Sibbaldia procumbens L.
Campanula uniflora L.
Erigeron uniflorus L.

(3) Not going above 12,500 or below 11,000 feet (3 species):—

Botrychium lunaria (L.).
Aster alpinus L.
Carex misandra R. Br.

(4) Not going above 12,500, but going below 11,000 feet (19 species):—

Phleum alpinum L.
Festuca pseudovina Hackel.
Carex nardina Fries.
C. alpina Sw.
C. capillaris L.
Lemna gibba L.
Juncus castan us Smith.
Vagnera stellata (L.).
Bistorta vivipara (L.).
Ranunculus affinis R. Br. (to Asia).
Thalictrum alpinum L.
Epilobium anagallidifolium Lam.
Moneses uniflora (L.).
Pyrola secunda L.
P. minor L.
P. uli g nosa Torrey (to Japan).
P. chlorantha Schwartz.
Utricularia vulgaris L.
Adoxa moschatellina L.

[1] In addition, *Alsine baicalensis* and *A. læta* are said to occur in Asia.

Muscaria adscendens (L.), according to Nelson, is different from our plant; in this case the latter must be removed from the circumpolar list, and will bear the name *Muscaria oregonensis* (*Ponista oregonensis* Raf., 1836).

It will be seen that of the Old World species, 26 go above 12,500 feet, and 13 do not go below 11,000. Seven, however, go below 8000. Admitting that the figures are only rough and approximate, it still comes out quite clearly that the circumpolar flora, while of course boreal, is not especially arctic-alpine. The most characteristic arctic plant is no doubt the Papaver, which seems curiously out of place in our flora.

Out of the 48 the following occur in the British Islands, which are neither arctic nor greatly elevated:—

Botrychium lunaria (L.).
Filix fragilis (L.).
Phleum alpinum L.
Poa alpina L.
Carex incurva Lightf.
C. alpina Sw.
C. atrata L.
C. rupestris All.
C. capillaris L.
Lemna gibba L.
Juncus castaneus Smith.
Juncoides spicatum (L.).
Oxyria digyna (L.).
Bistorta vivipara (L.).
Silene acaulis L.
Thalictrum alpinum L.
Saxifraga cernua L.
Dryas octopetala L.
Sibbaldia procumbens L.
Epilobium anagallidifolium Lam.
Pyrola secunda L.
P. minor L.
Utricularia vulgaris L.
Adoxa moschatellina L.
Sagina nivalis Fries.

Species Which go above 12,500 Feet, but are Confined to America

(1) Species which extend to British America or Alaska

(*a*) Species not reported below 11,000 feet (7 species):—

Poa arctica R. Br.
Salix petrophila Rydb.
Alsinopsis rossii (Richards).
A. quadrivalvis (R. Br.).
Ranunculus eschscholtzii Schl.
Draba fladnizensis Wulf.
Castilleja occidentalis Torrey.

Castilleja tincta (*C. pallida occidentalis tincta* Ckll., *Bull. Torr. Bot. Club*, 1890, p. 36) is doubtless a hybrid between *occidentalis* and *haydeni*.

(*b*) Species going below 11,000 feet (31 species):—

Deschampsia alpicola Rydb.
Poa crocata Mich. (Goes below 8000.)
Festuca brachyphylla Schultes.
Carex festiva Dewey. (Down to6500.)
C. petasata Dewey.
Juncus drummondii Mey.
Salix glaucops Anders. (Down to 7000.)
Alsinopsis propinqua (Richards).
A. obtusiloba Rydb.
Androsace carinata Torrey.
Anthopogon elegans (A. Nelson).
Phacelia sericea Hook.
Castilleja rhexifolia Rydb. (Down to 7000.)
Solidago ciliosa Greene.
Antennaria media Greene.
Draba crassifolia Graham.
Rhodiola integrifolia Raf.
Heuchera parvifolia Nutt.
Muscaria delicatula Small.
Leptasea austromontana (Wieg.). (Down to 6000.)
Potentilla quinquefolia Rydb.
P. dissecta Pursh.
P. uniflora Ledeb.
P. rubripes Rydb.
Atelophragma elegans (Hook.). (Down to 7000.)
Linnæa americana Forbes.
Arnica parryi A. Gray.
Senecio columbianus Greene. (Down to 5000.)
S. purshianus Nutt. (Down to 6000.)
Agoseris aurantiaca (Hook.). (Down to 6000.)
Taraxacum scopulorum (Gray).

The two species of Alsinopsis are modifications of well known circumpolar types. *A. propinqua* has been considered identical with *Alsinopsis hirta* (*Arenaria hirta* Wormsk.), which has itself been placed as a variety of *Alsinopsis verna* (*Arenaria verna* L.). *A. obtusiloba*, which my wife obtained in abundance on Arapahoe Peak, Colo., on Sept. 1 of the present year, is a segregate from *Alsinopsis sajanensis* (*Arenaria sajanensis* Willd.). *Sedum stenopetalum* Pursh, is given by Rydberg as only up to 12,000; but my wife found it far above timber line on Arapahoe Peak.

(2) Species which do not extend beyond the United States.

(*a*) Species not reported below 11,000 feet (35 species):—

Avena mortoniana Scribn. (Colo. only.)
Poa pudica Rydb. (Colo. only.)
P. alpicola Nash.
P. rupicola Nash.
P. grayana Vasey. (Colo. and Wyo. only.)
P. lettermannii Vasey. (Colo. and Wyo. only.)
Carex elynoides Holm. (Colo. only.)
Allium pikeanum Rydb. (Colo. only.)
Eriogonum aureum Nutt. (Colo. only.)
E. xanthum Small. (Colo. only.)
Paronychia pulvinata A. Gray.
Cerastium pulchellum Rydb. (Colo. only.)

Ranunculus ocreatus Greene. (Colo. only.)
Smelowskia lincariloba Rydb. (Colo. only.)
Erysimum nivale (Greene).
Draba chrysantha S. Wats. (Colo. and N. M. only.)
D. streptocarpa grayana Rydb. (Colo. only.)
D. decumbens Rydb. (Colo. only.)
Leptasea chrysantha A. Gray. (Colo. and N. M.)
Oreoxis humilis Raf.
Phlox condensata (A. Gray). (Colo. and N. M.)
Polemonium speciosum Rydb.
Eritrichium argenteum Wight.
Mertensia bakeri Greene. (Colo. only.)
M. alpina (Torrey). (Colo. only.)
Chionophila jamesii Benth. (Colo. and So. Wyo.)
Chrysopsis alpicola Rydb. (Colo. and Wyo.)
Antennaria sierræ-blancæ Rydb. (Colo. only.)
Artemisia scopulorum A. Gray.
A. monocephala (A. Gray). (Colo. only.)
A. saxicola Rydb. (Colo. and Wyo.)
Senecio soldanella A. Gray. (Colo. only.)
S. petrocallis Greene. (Colo. only.)
S. porteri Greene. (Colo. only.)
Carduus hesperius (Eastw.). (Colo. only.)

Of all these, certainly the most remarkable is the Chionophila. The large number of endemic alpine species is especially noteworthy. The earliest name for the dwarf alpine Erysimum is *E. asperum nanum* Ckll., (*Nature Notes*, 1891, p. 15). Above timber line on the Truchas Peaks of northern New Mexico is another endemic Mertensia, *M. cælestina* Nels. & Ckll.

(*b*) Species going below 11,000 feet (78 species):—

Poa reflexa V. & S.
P. pattersonii Vasey. (Colo., Ariz.)
P. epilis Scribn.
Agropyron scribneri Vasey.
Carex chalciolepis Holm. (Colo. only.)
Juncus parryi Engelm.
Salix pseudolapponum Seem. (Colo. only.)
S. saximontana Rydb.
Claytonia megarrhiza Parry.
Alsine baicalensis Coville (to Asia?)
Clementsia rhodantha (A. Gray).
Rhodiola polygama Rydb. (Colo., N. M.)
Telesonix jamesii (Torrey). (Colo. only.)
Saxifraga debilis Engelm.
S. simulata Small.
Spatularia vreelandii Small.
Trifolium nanum Torrey.
T. dasyphyllum Torrey. (Down to 7000.)
T. parryi A. Gray.
Sidalcea candida A. Gray. (Down to 7000.)
Epilolium ovatifolium Rydb.
Oreoxis bakeri C. & R. (Colo. only.)
Angelica grayi C. & R. (Colo. and So. Wyo.)
Primula angustifolia Torrey. (Colo. and N. M.)
P. parryi A. Gray. (Properly Hudsonian Zone.)

Swertia palustris A. Nels.
Phlox scleranthifolia Rydb.
P. cæspitosa Nutt.
Gilia pinnatifida Nutt. (Down to 4000.)
Polemonium scopulinum Greene. (Colo. only.)
P. grayianum Rydb. (Colo. only.)
P. confertum A. Gray. (Wyo., Colo.)
Bistorta bistortoides (Pursh.). (Down to 7000.)
Paronychia diffusa A. Nels. (Down to 5000.)
Arenaria fendleri A. Gray. (Down to 7000.)
A. fendleri porteri Rydb. (Down to 7000.)
Delphinium barbeyi Huth.
D. alpestre Rydb. (Colo. only.)
Anemone zephyra A. Nels.
Thlaspi glaucum A. Nels.
Erysimum radicum Rydb. (Colo. only.)
E. amænum (Greene.) (Colo. only.)
Draba parryi Rydb. (Colo., Wyo).
D. streptocarpa A. Gray. (Down to 6000.)
Potentilla minutifolia Rydb. (Colo. only.)
P. tenerrima Rydb. (Colo. only.)
P. saximontana Rydb. (Colo. only.)
Acomastylis turbinata (Rydb.).
Pentstemon hallii A. Gray. (Colo. only.)
P. harbourii A. Gray. (Colo. only.)
Besseya alpina (A. Gray.)
B. plantaginea Benth. (Down to 6000.)
Pedicularis grayi A. Nels.
P. scopulorum A. Gray. (Colo. only.)
Valeriana acutiloba Rydb.
Chrysothamnus pinifolius Greene. (Down to 7000; is 13,000 perhaps erroneous?)
Tonestus pygmæus T. & G.
Solidago decumbens Greene. (Wyo. and Colo.)
Townsendia rothrockii Gray.
Machæranthera pattersonii (Gray). (Colo. only.)
Aster andinus Nutt. (? Below 11,000.)
Erigeron pinnatisectus (Gray).
Antennaria umbrinella Rydb. (Down to 7500.)
A. viscidula A. Nels. (Wyo. and Colo.)
Tetraneuris lanata (Nutt.). (Down to 6000.)
Rydbergia grandiflora (T. & G.)
R. brandegei (A. Gray). (Colo. and N. M.)
Senecio amplectens A. Gray. (Colo. only.)
S. holmii Greene. (Colo. only.)
S. taraxacoides (A. Gray). (Colo. only.)
S. carthamoides Greene. (Colo. and Wyo.)
S. crassulus A. Gray.
S. atratus Greene. (Colo. only; down to 7500.)
S. harbourii Rydb. (Colo. only.)
S. rosulatus Rydb. (Colo. only; down to 5000.)
S. fendleri A. Gray.
S. crocatus Rydb. (Wyo. and Colo.)
Agoseris maculata Rydb. (Colo. only.)

Sidalcea candida is typical of the Canadian Zone; I have never seen it at timber line or above.

Species not Reported above 12,500 Feet nor below 11,000

(1) Species which extend to British America or Alaska (3 species):—

Draba cana Rydb.
Artemisia spithamæa Pursh.
Carduus hookerianus (Nutt.).

(2) Species which do not extend beyond the United States (19 species):—

Deschampsia curtifolia Scribn.
Poa phœnicea Rydb. (Colo. only.)
Carex chimaphila Holm. (Colo. only.)
C. engelmannii Bailey. (Colo. only.)
Arenaria tweedyi Rydb.
Draba graminea Greene. (Colo. only.)
Micranthes brachypus Small.
Trifolium salictorum Greene. (Colo. only.)
Swertia congesta A. Nels.
Gilia cephaloidea Rydb.
Eritrichium elongatum (Rydb.).
Mertensia picta Rydb. (Colo. only.)
M. parryi Rydb. (Colo. only.)
M. canescens Rydb. (Colo. only.)
Castilleja haydeni (A. Gray). (Colo. and N. M.)
Erigeron melanocephalus A. Nels.
Achillea alpicola Rydb.
Senecio invenustus Greene. (Colo. only.)
S. lapathifolium Greene. (Colo. only.)

Thus a restricted vertical range goes with a restricted latitudinal one as might be expected. *Castilleja haydeni* is exceedingly abundant just above timber line on the Sangre de Cristo range.

Species not Reported above 12,500 Feet but going below 11,000

(1) Species not reported below 8000 feet.

(*a*) Species which extend to British America or Alaska (31 species):—

Picea engelmanni (Parry).
Abies lasiocarpa (Hooker).
Trisetum majus (Vasey).
Poa leptocoma Bong.
Salix chlorophylla Anders.
Polygonum montanum (Small).
Alsine læta (Richards).
Cerastium beeringianum C. & S.
Mœhringia macrophylla (Hooker).
Caltha leptosepala Hooker.
Aconitum columbianum Nutt.
Pectianthia pentandra (Hooker).
Micranthes arguta (D. Don).
Potentilla pinnatisecta (S. Wats.).
Erythrocoma ciliata (Pursh).
Pyrola asarifolia Mx.

Vaccinium cæspitosum Mx.
V. poreohilum Rydb.
V. erythrococcum Rydb.
Chondrophylla americana (Engelm.).
Phacelia ciliosa Rydb.
Mimulus langsdorfii Sims.
Veronica wormskjoldii R. & S. (Goes above timber line in New Mexico.)
Castilleja lancifolia Rydb.
Elephantella grœnlandica (Retz.).
Pedicularis racemosa Dougl.
P. bracteata Benth.
Aster apricus (A. Gray).
Erigeron salsuginosus (Rich.).
Hieracium gracile Hooker.
Agoseris gracilens (A. Gray).

(*b*) Species confined to the United States, or not extending north of the British Boundary (71 species):—

Pinus aristata Engelm.
Stipa minor (Vasey).
Poa sheldonii Vasey. (Colo. only.)
Festuca minutiflora Rydb.
F. thurberi Vasey.
Carex melanocephala Turcz.
C. scopulorum Holm. (Colo. only.)
Anticlea coloradensis Rydb.
Polygonum commixtum Greene.
Oreobroma pygmæa (A. Gray).
Cerastium earlei Rydb. (Colo. only.)
C. occidentale Greene.
Trollius albiflorus (A. Gray).
Aquilegia saximontana Rydb. (Colo. only.)
Aconitum bakeri Greene.
Ranunculus unguiculatus Greene. (Colo. only.)
R. alismæfolius Geyer.
R. macauleyi A. Gray. (Colo. only.)
R. alpeophilus A. Nels.
R. adoneus A. Gray.
Thlaspi nuttallii Rydb.
Smelowskia americana Rydb.
Pentstemon glaucus Graham.
Castilleja lauta A. Nels.
C. linearis Rydb. (Colo. only.)
C. puberula Rydb. (Colo. only.)
Pedicularis parryi A. Gray.
Campanula parryi A. Gray.
Macronema discoideum Nutt.
Aster fremontii A. Gray.
Draba crassa Rydb.
D. spectabilis Greene.
D. luteola Greene. (Colo. only.)
Micranthes arnoglossa (Greene).
Ribes lentum (Jones).
Lupinus parviflorus Nutt.
Trifolium brandegei S. Wats. (Colo. only.)
T. stenolobum Rydb. (Colo. only.)
T. lividum Rydb.[1]
Geranium pattersonii Rydb. (Colo. only.)
Viola bellidifolia Greene.
Oreoxis alpina (A. Gray).
Ligusticum porteri C. & R.
Pseudocymopterus montanus (A. Gray).
P. sylvaticus A. Nels.
Androsace subumbellata (A. Nels.).
Anthopogon barbellatus (Engelm.). (Colo. only.)
Amarella monantha (A. Nels.). (Colo. only.)
A. scopulorum Greene.
A. plebeja holmii (Wettst.).

[1] *Trifolium lividum* is given by Rydberg as extending to 12,000 feet; my wife found it on Arapahoe Peak about timber line.

Dasystephana parryi (Engelm.).[1]
Phlox kelseyi Britton.
Polemonium delicatum Rydb. (Colo., N. M.)
Mertensia polyphylla Greene.
Erigeron leucotrichus Rydb.
E. leiomerus A. Gray.
E. elatior A. Gray.
E. coulteri Porter.
E. salsuginosus glacialis (Nutt.).
E. viscidus Rydb. (Colo. only.)
Antennaria nardina Greene.
Arnica silvatica Greene.
A. rydbergii Greene.
A. tenuis Rydb.
A. subplumosa Greene.
Senecio pagosanus Heller. (Colo. only.)
S. blitoides Greene. (Colo. only.)
S. pentodontus Greene.
Carduus scopulorum Greene. (Colo. only.)
C. griseus Rydb. (Colo. only.)
Agoseris pumila (Nutt.).

To these may be added the two following:—

Mertensia perplexa Rydb. Arapahoe Peak, Colo., in a draw just above timber line (*W. P. Cockerell*).

Senecio triangularis Hooker. Arapahoe Peak, at timber line (*Dr. F. Daniels* and *W. P. Cockerell*).

(2) Species going below 8000 feet. In the case of some of these, the range to 12,000 feet may need confirmation. It is not impossible that misunderstandings have sometimes arisen, as the result of vague labeling.

(*a*) Species extending to British America or Alaska (24 species):—

Equisetum lævigatum A. Br.
Calamagrostis purpurascens R. Br. (To Greenland.)
Festuca ingrata (Hack.).
Agropyron violaceum (Hornem.). (To Greenland.)
Carex ebenea Rydb.
Anticlea elegans (Pursh).
Eriogonum flavum Nutt.
Anemone globosa Nutt.
Ranunculus ellipticus Greene.
Thalictrum venulosum Trelease.
Sedum stenopetalum Pursh. (But really goes higher than Rydberg reports.)
Ribes parvulum (A. Gray).
Lepargyræa canadensis (L.).
Osmorrhiza obtusa (C. & R.). (*Washingtonia obtusa* C. & R.)
Androsace puberulenta Rydb.
Amarella strictiflora (Rydb.).
Dasystephana affinis (Griseb.).
Veronica americana Schwein.
Campanula petiolata D. C.
Erigeron multiflorus Rydb.
E. glabellus Nutt.
Antennaria aprica Greene.
Achillea lanulosa Nutt.
Lygodesmia juncea (Pursh).

[1] Mixed with this according to Greene, is a second species, *Dasystephana bracteosa* (*Gentiana bracteosa* Greene, *Pitt.*, vol. 4, 180.)

The Campanula and Achillea are offshoots from Old World types, and were until recently considered identical with them.

(*b*) Species not going north of the British Boundary (32 species):—

Blepharineuron tricholepis (Torrey). (To Mexico.)
Poa longipedunculata Scribn.
P. pratericola Rydb. & Nash.
P. buckleyana Nash.
Eriogonum umbellatum Torrey.
Cerastium pilosum Greene. (Colo. only.)
C. oreophilum Greene. (To California.)
Arenaria confusa Rydb.
Silene hallii S. Wats.
Aquilegia cærulea James.
Erysimum wheeleri S. Wats.
Heuchera hallii A. Gray. (Colo. only.)
Micranthes rhombifolia (Greene).
Ribes wolfii Rothr.
Drymocallis fissa (Nutt.).
Viola canadensis neomexicana (Greene).
Gayophytum racemosum T. & Q.
Polemonium brandegei (A. Gray). (Colo. only.)
Phacelia alpina Rydb.
Mertensia pratensis Heller.
M. viridula Rydb. (Colo. only.)
Besseya ritteriana (Eastw.). (Colo. only.)
Sambucus microbotrys Rydb.
Chrysopsis arida A. Nels.
Oreochrysum parryi A. Gray.
Erigeron glandulosus Porter.
E. superbus Greene. (Colo. only.)
Dugaldia hoopesii (A. Gray).
Arnica monocephala Rydb.
Senecio pudicus Greene. (Colo. only.)
Carduus oreophilus Rydb. (Colo. only.)
Agoseris agrestis Osterh. (Colo. only.)

Taking the whole list of species which reach 12,000 feet, arranged in systematic order, we note many points of interest.

(1) There is only one fern, a circumpolar species.

(2) The grasses number 33, of which four are circumpolar, but others are very close to Old-World types. There is an appreciable element of endemic alpine grasses.

(3) The Cyperaceæ number 20, of which 11 reach the Old World. All but one (Elyna) belong to Carex.

(4) Of the four Juncaceæ, two are circumpolar. For a very interesting account of the allies of *Juncoides spicatum* in Africa, see Engler in *Ann. Bot.*, Oct., 1904.

(5) In Portulacaceæ, the peculiar alpine *Claytonia megarrhiza* is noteworthy. It belongs to a distinct subgenus which ranges from Asia into our Rocky Mountains.

(6) The Alsinaceæ are numerous (18 species); one (*Sagina*

nivalis) is circumpolar. *Alsine baicalensis* appears to have a singular distribution; north to Montana and Oregon only, and then reappearing in Central Asia. It may be that the identity of the Asiatic and American plants needs confirmation. *Alsine læta* is supposed to reach Siberia, though Rydberg says nothing of its ranging beyond our continent.

(7) The Ranunculaceæ are well represented (21 species), but are mostly of the Hudsonian Zone rather than the Arctic-Alpine; 16 do not range above 12,000 feet.

(8) The Cruciferæ are represented by Thlaspi (4), Smelowskia (2), Erysimum (4), and Draba (13). Only *Draba aurea* appears to be circumpolar.

(9) The Rosaceæ include as many as 9 species of Potentilla. Of the 14 species of this family, only 3 fail to go above 12,500 feet.

(10) The Leguminosæ include no circumpolar types, and only one reaches British America; 7 out of the 9 belong to Trifolium.

(11) The Epilobiaceæ number only 3; *Chamænerion angustifolium* (L.) should probably be added, as my wife found a reduced form of it above timber line on the Truchas Peaks in New Mexico.

(12) Of the 8 Umbelliferæ none is circumpolar, and only one appears to reach British America.

(13) Of the 6 Pyrolaceæ, four are circumpolar, and a fifth reaches Japan. The species of Pyrola exhibit a remarkable degree of stability.

(14) No Ericaceæ, in the restricted sense, are in the list, but I believe *Kalmia microphylla* (Hooker) should be there.

(15) The Gentianaceæ number 12; while only one is supposed to extend to the Old World, others are very close to Asiatic and European species. *Anthopogon elegans* was formerly not separated from *Anthopogon dentosus* (*Gentiana dentosa* Rottb.). *Amarella monantha* was considered by Gray inseparable from *Amarella tenella* (*Gentiana tenella* Rottb.). *Amarella strictiflora* was considered a form of *Amarella amarella* (*Gentiana amarella* L.). *Chondrophylla fremontii* was referred to *Chondrophylla humilis* (*Gentiana humilis* Stev.). *Dasystephana romanzovii* was not separated from *Dasystephana frigida* (*Gentiana frigida* Haenke). The species of Swertia were included in *S. perennis* L.

(16) The Polemoniaceæ consist of four species of Phlox,

two of Gilia, and six of Polemonium. Not one reaches the Old World, or even, apparently, British America.

(17) The Boraginaceæ include two species of Eritrichium and ten of Mertensia; all peculiar to the western United States but closely allied to arctic species.

(18) Of the 23 Scrophulariaceæ, nine reach British America (two even Greenland), but none is circumpolar. *Veronica wormskjoldii*, however, is a slightly modified form of the type represented in Europe by *V. alpina* L. *Veronica serpyllifolia* L., a truly circumpolar species, occurs in Colorado only up to 11,000 feet, according to Rydberg. I found it on the top of the Las Vegas Range in New Mexico, at 11,000 feet, June 28, 1902. The plants were, however, divergent from typical *serpyllifolia*, representing a new variety or subspecies *neomexicana*, about 15 cm. high, puberulent, flowers deep blue, calyx lobes oblong, obtuse.

(19) *Linnæa americana* and *Campanula petiolata* are only slightly modified representatives of Old-World types.

(20) The Compositæ are very numerous, 79 species. The two largest genera are Erigeron (14 species) and Senecio (24 species). Carduus has 5, Arnica 6, Artemisia 4, Antennaria 6, Aster 4, Solidago 2. These are circumpolar genera; but there are some endemic genera, partly of austral derivation, the most remarkable of which is Rydbergia.

(21) The following families, represented in the Colorado flora, are wholly absent from our list of species reaching 12,000 feet.

Marsileaceæ (7720).
Isoëtaceæ (8150).
Lycopodiaceæ (10,500).
Juniperaceæ (10,000).
Ephedraceæ (7000).
Typhaceæ (6000).
Sparganiaceæ (11,500).
Zanichelliaceæ (11,500).
Naiadaceæ (5100).
Scheuchzeriaceæ (10,000).
Alismaceæ (9000).
Elodiaceæ (6500).
Araceæ (4500).
Commelinaceæ (6500).
Pontederiaceæ (5500).
Dracænaceæ (8000).[1]
Calochortaceæ (10,000).
Trilliaceæ (9000).
Smilacaceæ (6000).
Ixiaceæ (10,000).
Orchidaceæ (11,500).
Monotropaceæ (8000).

[1] Rydberg gives *Yucca glauca* as only reaching 6000 feet; this is erroneous, as it reaches 8000 at Florissant and elsewhere. Rydberg's maximun for the family is 6500.

Ericaceæ (11,000).
Oleaceæ (5000).
Menyanthaceæ (8000).
Heliotropaceæ (4800).
Verbenaceæ (7500).
Labiatæ (Lamiaceæ) (10,000).
Solanaceæ (10,000).
Betulaceæ (11,000).
Corylaceæ (8000).
Fagaceæ (11,000).[1]
Urticaceæ (9000).
Cannabinaceæ (8000).
Ulmaceæ (6000).
Loranthaceæ (8850).
Santalaceæ (8000).
Chenopodiaceæ (10,000).
Amaranthaceæ (10,000).
Allioniaceæ (9000).
Tetragoniaceæ (8000).
Ceratophyllaceæ (Platte River).
Nymphæaceæ (11,000).
Berberidaceæ (10,000).
Fumariaceæ (10,000).
Capparidaceæ (9000).
Parnassiaceæ (11,000).
Hydrangeaceæ (10,000).
Malaceæ (11,000).
Amygdalaceæ (9500).
Mimosaceæ (3920).
Cassiaceæ (7000).
Apocynaceæ (9500).
Asclepiadaceæ (9000).
Cuscutaceæ (7000).
Convolvulaceæ (7000).
Orobanchaceæ (11,000).
Martyniaceæ (5340).
Plantaginaceæ (10,000).
Linaceæ (10,000).
Oxalidaceæ (9000).
Zygophyllaceæ (5340).
Rutaceæ (5400).
Polygalaceæ (5000).
Euphorbiaceæ (8000).
Callitrichaceæ (5340).
Limnanthaceæ (6500).
Spondiaceæ (8000).
Celastraceæ (10,000).
Aceraceæ (9000).
Frangulaceæ (9000).
Vitaceæ (9000).
Elatinaceæ (Platte River).
Frankeniaceæ (5340).
Hypericaceæ (10,000).
Cistaceæ (Douglas County).
Loasaceæ (10,000).
Cactaceæ (11,000).
Lythraceæ (6000).
Gunneraceæ (10,000).
Hederaceæ (9000).
Cornaceæ (10,000)..
Rubiaceæ (10,000).
Cucurbitaceæ (5100).
Lobeliaceæ (5200).
Ambrosiaceæ (8000).

The numbers following the family names indicate the highest altitude in feet to which the families ascend in Colorado according to the data given by Rydberg.

[1] *Quercus nitescens* Rydb., 11,000. This is very high for an oak. Although oaks are so abundant at Manitou, we found none at Florissant, 8000 feet. They go higher, however, in the Sangre de Cristo range.

BLOOD GILLS OF *SIMULIUM PICTIPES*

THOMAS J. HEADLEE

It is a well known fact that during larval life many aquatic insects possess gills. These have been regarded as thin transparent extensions of the body wall, which may or may not contain tracheæ. In one type of insect gill, the organ is abundantly supplied with tracheæ, and the evident function of the organ is the purification of the air contained in the tracheæ. Such a gill is known as a tracheal gill. In the other type, known as a blood gill, it is blood within the gill that is purified.

Whether there exist in pterygote insects true blood gills in the narrow application of this definition, is still an open question. Such organs have been described as present in many groups, notably in the larvæ of Trichoptera and Diptera. Those interested in the general discussion of the subject may find a concise but excellent *résumé* of the work done in Kolbe ('93) and Packard ('98).

Few of these so called blood gills have, however, been subjected to morphological examination. It is the purpose of the present paper to discuss from this view-point these structures of the larva of *Simulium pictipes* Hagen, a species of black-fly abundant in the streams about Ithaca, New York, but I shall first consider some of their grosser variations which appear in other species of Simulium.

Projecting from the anus on the dorsal side of the last abdominal segment, there may be seen in the living black-fly larva, three white, soft, curved filaments, which are in some species simple and in others branched. As long ago as 1823, Verdat called attention to these structures and gave good figures of the lateral and dorsal views of the larva of *Simulium sericium* Fries, showing three unbranched gills arising from the dorsal side of the posterior end of the body. His figures have been copied by a number of writers. Graber ('77) figured the unbranched gills of the larval *Simulium columbaczense* Schönb. C. V. Riley ('87) figured two types —

the unbranched filaments of *Simulium meridionale* Riley, and the branched structures of *Simulium pecuarum* Riley. Curiously enough, although figuring the gills in their correct position, Riley states in his general discussion that they occur on the under side of the body — a statement made by Osten Sacken sixteen years earlier, although even he contradicted himself by copying the figures of Verdat. In addition to these there have been figured, by Meinert ('86), who refers to them as anal papillæ, the unbranched gills of *Simulium ornatum* Meigen, by Townsend ('93) the branched type of a species of Simulium from the Grand Cañon of Colorado, by Lugger ('96) the simple type of *Simulium tribulatum* Lugger, and by Johannsen (:03) the unbranched type of *Simulium hirtipes* Fries.

Miall and Hammond seem to have been the first to call attention to the fact that these structures are retractile into the rectum, a fact which may be verified by study of living, or better, sectioned, specimens.

Most writers agree that these filaments are gills but there is a divergence of opinion regarding the method by which they function. Planchon ('44), Osten Sacken ('70), Riley, Townsend, and Comstock ('95) considered them as tracheal gills, Osten Sacken, Riley, and Osborn even stating that they connect with large internal tracheæ. Miall and Hammond, and Johannsen, on the other hand, regarded them as blood gills and without tracheæ. Such is the condition of our knowledge concerning this mode of respiration of Simulium larvæ. No connected work on the finer anatomy of their gills has been published. Such mention of the subject as occurs is confined to the gross anatomy and is scattered through accounts of life histories and descriptions of species.

In undertaking a more detailed study of the subject as exemplified in *Simulium pictipes*, both living and sectioned larvæ have been examined. For the study of the tracheæ found in the region of the gills it is very helpful to examine living larvæ, as in fixed material the lack of air in these passages makes it hard to see their finer branches. Most of the histological details were, of course, gained through a study of sections. To prepare these, larvæ were killed and fixed in Flemming's mixture, in hot and cold absolute alcohol, and in hot and cold Gilson's fluid. The hot alcohol and

hot Gilson's fluid were about equally successful. The material killed in the former cut easily but showed some shrinkage, while that prepared with the latter cut less easily and showed less shrinkage. The Flemming material cut so poorly that the preparations made from it were of little value. By staining on the slide with Gage's hæmatoxylin and orange G, the tissues were well differentiated.

In the living larva the gills are white, soft, and translucent, and

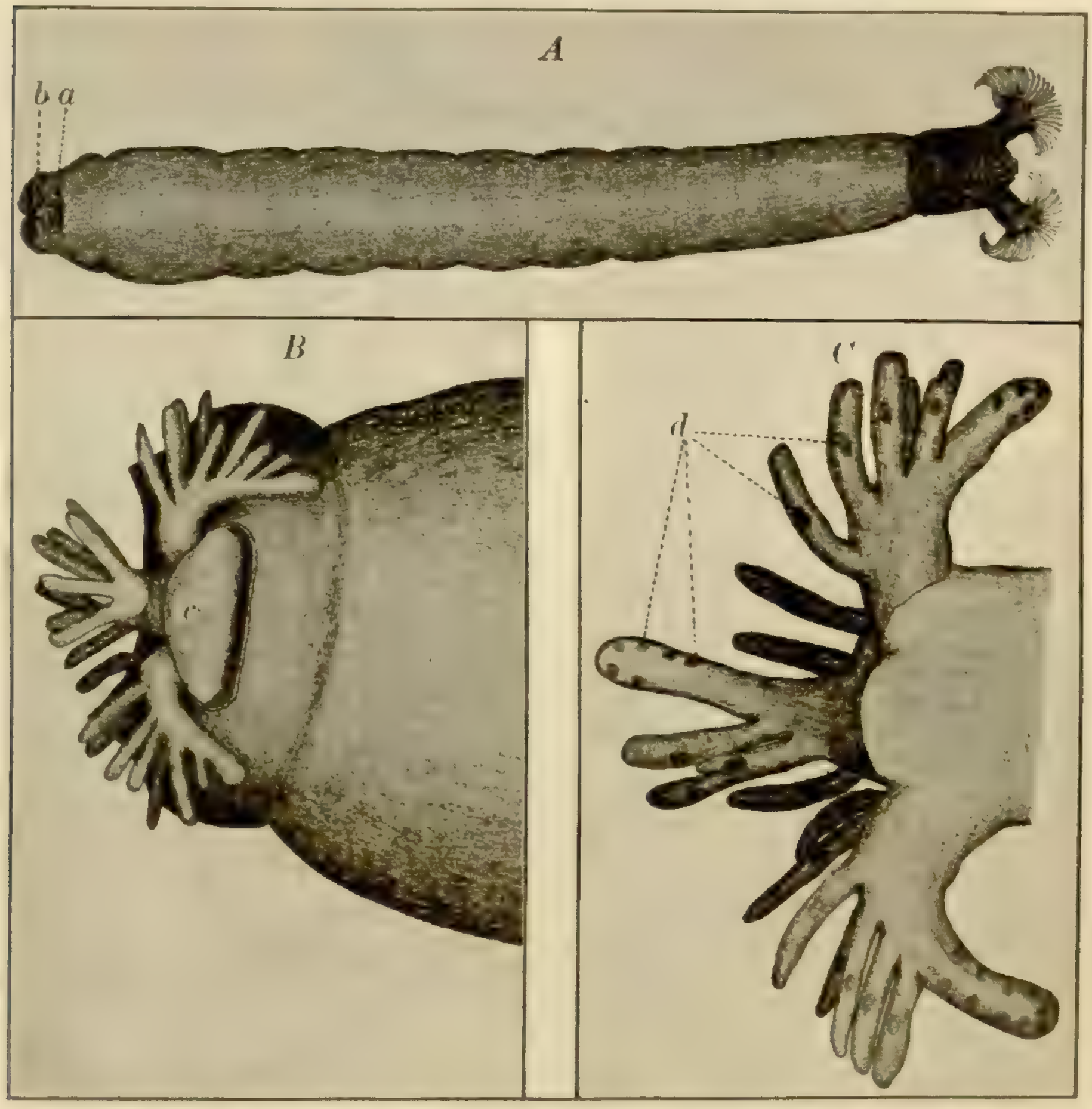

FIG. 1.— A. Dorsal view of the larva of *Simulium pictipes*, (× 8). B. Dorsal view of the posterior end of the larva showing the gills projecting from the anus, (× 13). C. Projected gills, showing the main filaments, finger-like branches, and some of the nuclei in each, (× 57). *a*, anus with slightly projecting gills; *b*, strongly chitinized X-shaped piece; *c*, dorsal wall of the rectum which has been everted and covers the bases of the gills; *d*, nuclei of main and branch filaments.

appear on the dorsal side of the last abdominal segment, just anterior to a dark, strongly chitinized, X-shaped piece (Fig. 1, A, *a*, *b*). They are projections of the ventral wall of the rectum and lie, when retracted, completely within the rectal cavity (Fig. 2, A).

They consist of three main filaments arising from the ventral rectal wall, each about 400 μ long and 120 μ wide at the base, tapering to 75 μ near the middle and to 60 μ at the distal end, and each furnished with many finger-like branches arising from their lateral and ventral walls (see Fig. 1, B.).

As might be expected from their morphological relationship,

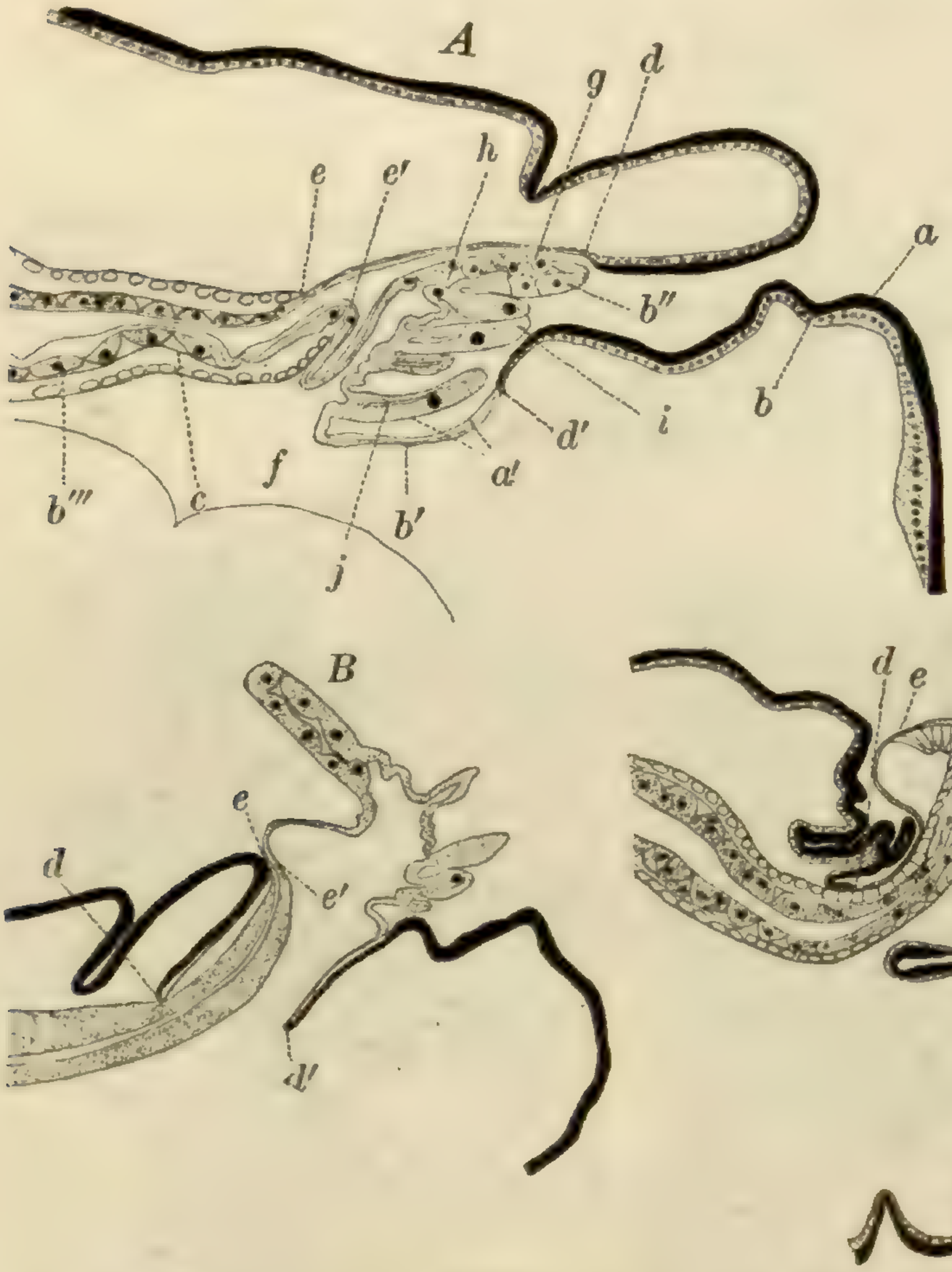

FIG. 2.— A. Sagittal section of the posterior end of the larva showing the gill within the rectum and showing the relation of its component layers to those of the rectum, (× 52). B. Similar section showing the gill projecting, (× 52). C. Similar section showing the gill projecting to its fullest extent. (× 53). *a*, cuticle of body wall; *a′*, intima of rectum and gill; *b*, hypodermis; *b′*, rectal epithelium; *b″*, gill epithelium; *b‴*, normal hind-intestinal epithelium; *c*, basement membrane; *d*, and *d′*, transition from body wall to rectal layers on the dorsal and ventral sides respectively ; *e* and *e′*, transition from rectal to normal hind-intestinal layers on the dorsal and ventral sides respectively; *f*, body cavity; *g*, main filament; *h*, cavity of main filament; *i*, finger-like branch; *j*, cavity of branch.

the gills are composed of the same three layers as is the rectum; the intima on the surface, the epithelium next, and the basement membrane adhering closely to the epithelium and lining the gill cavity. The intima is exceedingly thin, perfectly transparent and

without apparent structure. The epithelium is a layer varying in thickness from 5 μ to 18 μ, composed of large, distinct, somewhat flattened cells well filled with cytoplasm, and containing each a single large nucleus, in which the nucleolus and chromatin markings are very distinct. The chromatin occurs throughout the nucleus but is distributed a little more thickly around the periphery (Fig. 3, A and C). The basement membrane is very thin and much like that found under the hypodermis (Fig. 2, A).

At the point of union between the body wall and the rectum there is a marked decrease in the thickness of the layers, the intima and epithelium being much more delicate than the cuticle and hypodermis; and this condition is continued to a point some distance cephalad of the gill (Fig. 2, A) except that the epithelium of the gills is thicker than that of the chamber containing them. The basement membrane continues from the hypodermis through the gill without noticeable change.

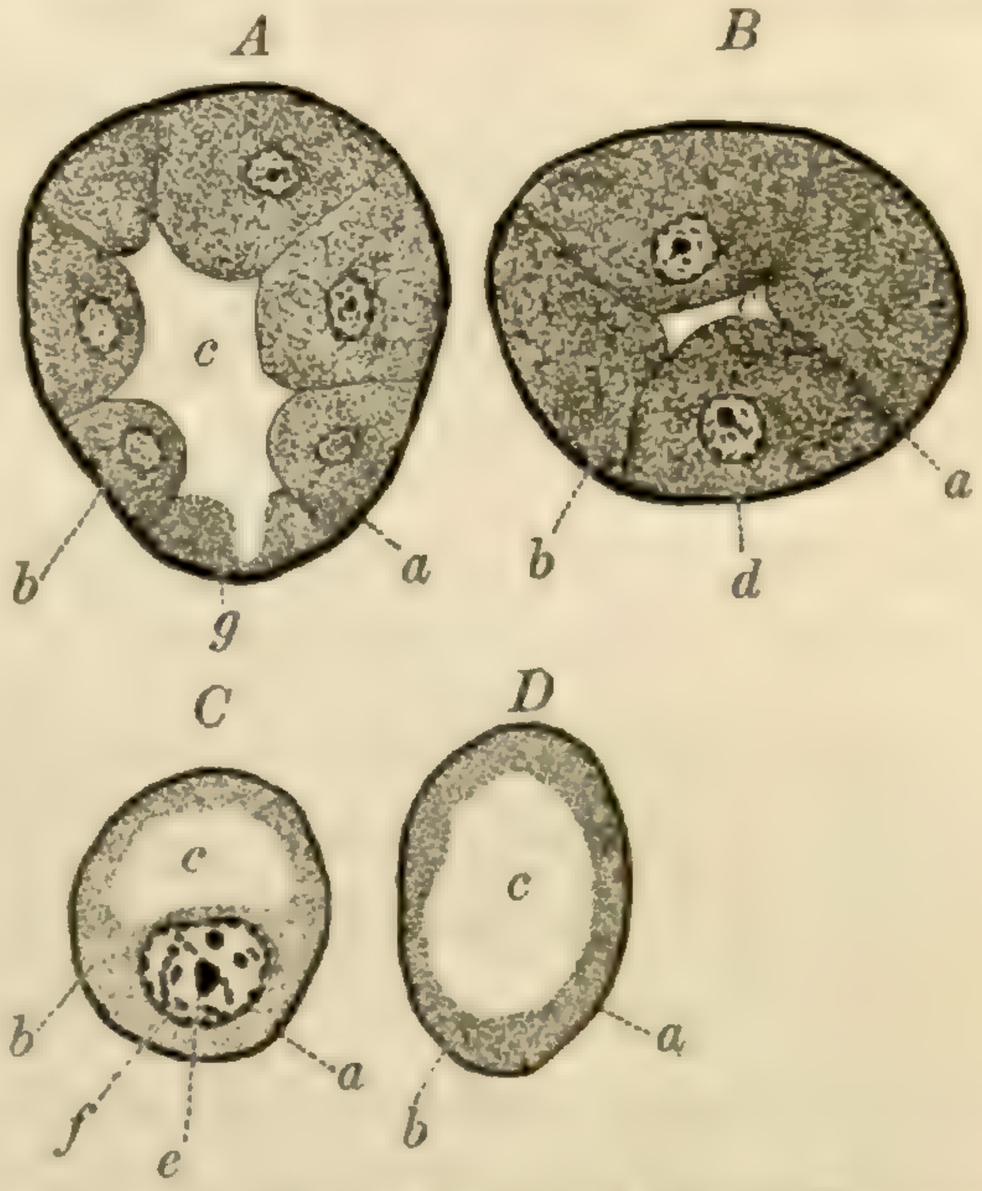

FIG. 3.— A. Cross section of a main filament taken at a point midway between the base and distal end, (× 255). B. Similar section taken near distal end, (× 255). C. Cross section of a finger-like branch taken in the region of the nucleus, (× 255). D. Similar section taken between nucleus and base, (× 255). *a*, intima; *b*, epithelium; *c*, cavities of both branch and main filaments; *d*, nucleus; *e*, nucleolus; *f*, chromatin granule; *g*, base of a finger-like branch.

The cells lining the distal end of the main filament are slightly larger than those at the base (Fig. 3, A, B). Each finger-like branch is composed of a single large cell, the base of which helps to form the wall of the main filament (Figs. 2, A, and 3, A). These branch cells are much larger than the main filament cells and contain larger nuclei, in which the chromatin particles more distinctly appear (Fig. 3, A, B, C). The nuclei are generally located near the middle in the cells of both the branches and the main filaments, but in the branches they are often nearer one side than the other. The nucleus, covered by a thin layer of

cytoplasm, occasionally projects into the cavity which penetrates the branch. The gill cavities occupy the main filaments, penetrate the branches, and communicate freely with the body cavity at the base of the gills. Found within these chambers are masses of slender tracheæ and as their presence in these organs strongly suggests that they do not function wholly as blood gills, I shall discuss them in detail.

During the larger part of the time I spent in this work, I believed tracheæ to be wanting in these gills, but masses of fine tube-like structures which appeared in the sections excited doubt. Having secured some living larvæ, I cut off, after many unsuccessful attempts, a projected gill. This being quickly mounted and examined with a $\frac{1}{6}$-inch objective and 1-inch ocular, there appeared reaching up into the gill cavities, masses of fine tracheal tubes filled with air. While they enter all parts of the basal opening, they are thickest in four main bands, two entering the central lobe and one each of the lateral lobes. This collection into bands might result from mechanical causes but, as a similar arrangement appeared in the sectioned material, it seems probable that it is the natural condition. The tubes are small, about $1\,\mu$ in diameter, of uniform size, and rarely branching unless in contact with the wall. They penetrate all parts of the gill cavity, and generally one and frequently two slender tracheæ lying close to the wall penetrate to the very tip of a unicellular branch. When viewed with a $\frac{1}{12}$ oil-immersion lens there may be seen in mounted and stained sections, given off from these tracheæ which lie close to the wall, fine branches penetrating the protoplasm. These air vessels gradually decrease in size as they approach the ends of the cavities. Just below the base of the gills they average $2\,\mu$ in diameter, half way up the main lobe they are about $1\,\mu$, and near the ends of the finger-like branches they have decreased to a diameter of $0.8\,\mu$. These measurements were taken while the tubes were filled with air.

The tracheæ branch very rarely in the gill cavity and in such cases as I have observed, the resulting branches were each about as large as their common parent. I have seen no tracheal trunks in the gill cavities, although they appear below in the body cavity and in many cases the slender tracheæ penetrating the gills have been traced to them.

While it has not been possible to see the actual blood movement in the projected gills, the abundance of blood-mass which appears in the sections in all parts of their cavities clearly demonstrates its presence there.

The gills may be projected or retracted at the will of the animal. When out, the middle filament projects dorso-cephalad, the side filaments dorso-latero-cephalad, and all the branches are thrown free into the swiftly flowing water which is the normal habitat of the animal (Fig. 1, B). The projection of the gills includes not only a movement of the organs themselves but also of the rectum. The usual amount of movement is shown in Fig. 2, A and B. Points *e* and *e'* represent the beginning of the normal intestinal epithelium on the dorsal and ventral sides respectively, while *d* and *d'* represent the beginning of the body wall on the same respective sides. In Fig. 2, A, the gills are retracted, while in Fig. 2, B, they are projected as much as the healthy animal usually protrudes them. In Fig. 2, B, *e* and *e'* have moved to the dorsal surface of the body, while *d* and *d'* have retained almost the same position. Sometimes, however, the living animal may project the gills to the extent illustrated in Fig. 2, C, and when killed in hot alcohol generally does so. This protrusion differs from that of the ventral sacs in the Thysanura, where the sac is simply turned wrong side out, for these are projected without being everted.

These gills are almost if not completely withdrawn when the animal is moving, and project freely only when it is fastened by its caudal sucker. They are rarely quiet when projecting but are usually moving a little way in or out.

I have found no muscular apparatus by the action of which the gills could be projected, but have been able to make them protrude by pressure exerted progressively from in front backward, and, as I have found the blood-mass in sections of protruded gills, it seems only reasonable to conclude that the gills are pushed out by an inflow of blood under such pressure as might be exerted by a contraction of the body muscles.

The gills are retracted by striated muscles which do not, so far as I can determine, penetrate their cavities. At least eight muscle bands are inserted on or near the bases of the gills, and each plays some part in the retraction of those organs. To aid my descrip-

tion of these muscles, I have made a diagram (Fig. 4) to show their position in the body of the animal, and have designated those of the left side in the order of their insertion passing from left to right, by the letters *a*, *b*, *c*, and *d*, and the corresponding ones of the right side, also in the order of their insertion passing from right to left, by the letters *a'*, *b'*, *c'*, and *d'*. Muscle *a*, which has a diameter of about 35 μ just before branching, is as large as any of the gill retractors. It is fastened to the basal region of the left gill by three branches. One is inserted in the lateral, another in the dorso-lateral, and a third in the ventro-lateral aspect of the

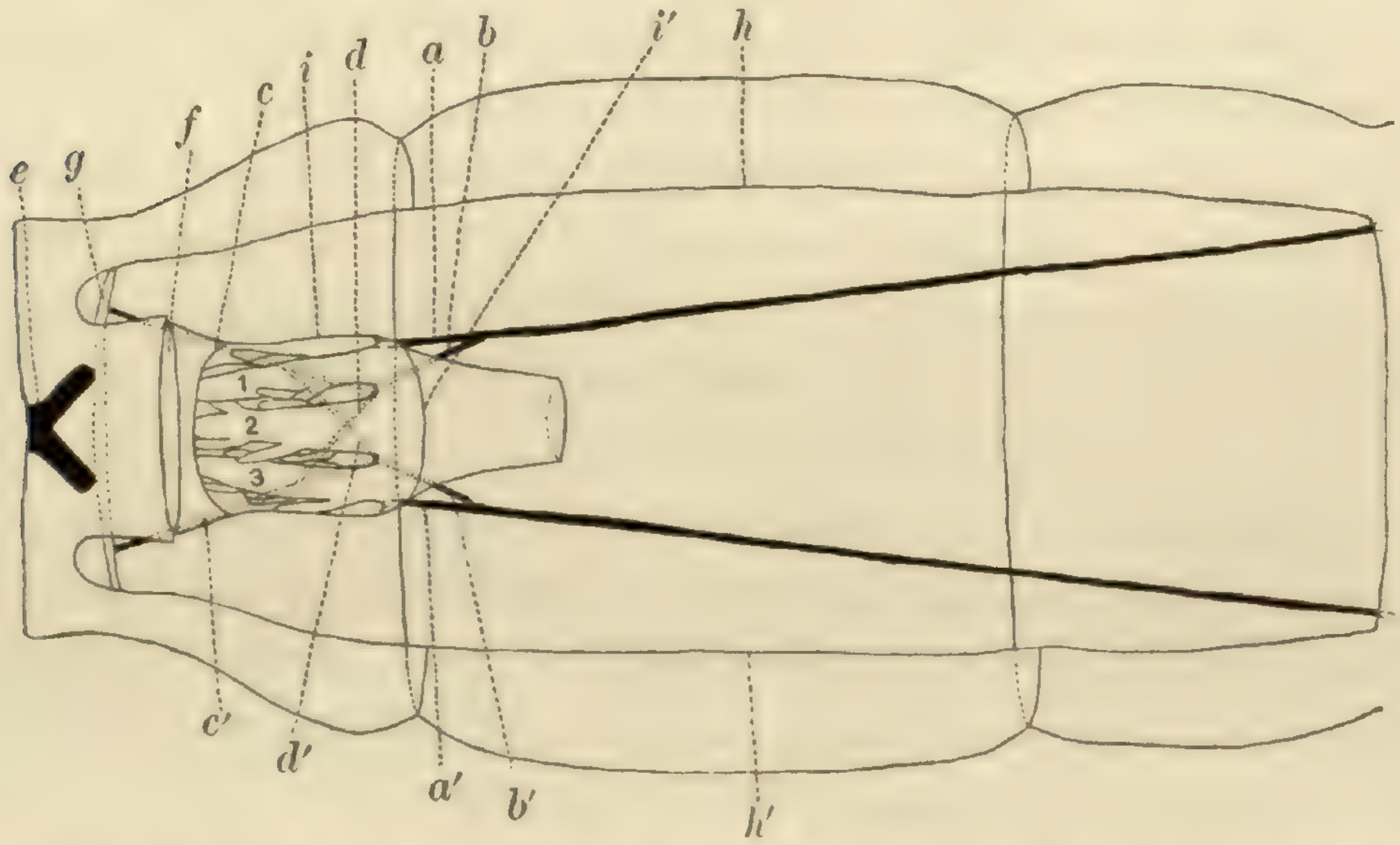

FIG. 4.— Diagram of the muscles which retract the gills. The dorsal wall of the body is cut away along lines *h* and *h'* and a part of the dorsal wall of the rectum is cut away along lines *i* and *i'*. The ventral wall of the body is exposed by the first and the floor of the rectum upon which the gills lie by the second operation. *1*, *2*, and *3*, the left, central, and right gills; *e*, strongly chitinized X-shaped piece; *f*, anal opening; *g*, infolding of the body wall lying on the abdominal floor just cephalad of the caudal sucker.

left gill base. Of these, the second is both the largest and most clearly inserted. These branches pass cephalad and quickly fuse to form *a*, which passes dorso-cephalad and slightly laterad until it finally fastens to the ventral aspect of the dorsal wall of the abdomen. After the junction of the three branches forming *a* and before it reaches its point of origin, it is joined by muscle *b* and later by a large muscle band from the anal region. Muscle *b*, which is also a large conspicuous band of about 27 μ diameter, is inserted in the ventral aspect of the tissue between the left and

central gill bases. From thence it passes dorso-cephalad and laterad until it joins muscle *a*. Muscle *c*, a smaller, yet plainly marked band of about 12 μ diameter, is inserted in the gill at the same point as *b*, and extends ventro-caudad and slightly laterad until it reaches the floor of the abdomen where it attaches to an infolding of the body wall. This infolding extends transversely across the abdominal floor just cephalad of the caudal sucker. Muscle *d*, the diameter of which is slightly less than that of *c*, is inserted just mesad of *c* and extends ventro-caudad and mesad until it fuses with muscle *c'* of the right side.

As the muscles of the right side correspond to those of the left they require no separate discussion.

When the gills are pushed out, the muscles are drawn with the base into the everted part of the rectum, and when they contract the gills are pulled back to their place inside.

The presence of functional tracheæ in their cavities points to the conclusion that these organs must, in some degree, function as tracheal gills; for, if they act only as blood gills, the epithelial cells, inasmuch as the oxygen before reaching the blood must pass through their substance, would need no tracheation. But the comparatively small number and size of the tracheæ supplied to the gills, together with the undoubted presence of blood in their cavities, render untenable the hypothesis that they function wholly as tracheal gills.

In the light of this work it is evident that, except in a remote morphological sense, not all gills are extensions of the body wall but that some are borne by the rectum, and it is also evident that not all insect gills act wholly either as tracheal or as blood gills, but that some function as both.

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